HIGHER-LEVEL RELATIONSHIPS OF THE SPIDER FAMILY CTENIDAE (ARANEAE: CTENOIDEA)

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ABSTRACT

A cladistic analysis based on parsimony is undertaken to test hypotheses concerning the monophyly of the ctenid spiders and the relationships among their various clades. The data matrix comprised a total of 98 species representing 16 families scored for 146 characters, with all but six taken from various morphological systems; the remaining are behavioral attributes.

Ctenidae is shown to be polyphyletic as currently delimited, but the most severely questioned taxa (i.e., *Acanthoctenus*, *Cupiennius*, and *Ancylometes*) are indeed members of this family. The so-called ctenid eye pattern is shown to be a synapomorphy uniting a more restricted set of taxa. This clade is recognized as Ctenidae sensu stricto and it comprises at least five major lineages: Acantheinae, Acanthocteninae, Calocteninae, Cteninae, and Viridasiinae. The latter taxa are hypothesized to be the sister group of all other ctenids. In turn, a clade formed by Miturgidae s.s. and Zoridae s.s. is proposed as the sister group of Ctenidae. The cladistic analysis also refutes the monophyly of *Ctenus*, *Anahita*, *Enoploctenus*, *Celaetycheus*, and *Leptoctenus*.

The following taxonomic changes are proposed: *Anahita isaloensis* Ono, 1993 is transferred to *Vulsor* Simon, 1888; *Diallomus* Simon, 1897, currently placed in Zoridae, is transferred to Ctenidae; *Tunabo* Chamberlin, 1916 is synonymized with *Neoctenus* Simon, 1897; *Neoctenus* is removed from Zoridae and transferred to Trechaleidae; *Xenoctenus* Mello-Leitão, 1938 is removed from the synonymy of *Tunabo* and considered incertae sedis, within Ctenoidea.

INTRODUCTION

Despite their species richness and abundance, especially in tropical forests of Africa and South America, ctenid spiders are far from well known. Some taxonomic problems arise in placing new species into currently known genera, and also in grouping those genera into a suprageneric classification. Furthermore, the type specimen of *Ctenus dubius* Walckenaer, 1805 is lost (F.O.P.-Cambridge, 1897a: 57) and its original description could easily apply to members of such disparate genera as *Oligoctenus* Simon, 1887, *Phoneutria* Perty, 1833, or *Ancylometes* Bertkau, 1880, with the latter being currently placed in Pisauridae. The lack of a type specimen and a good description has encouraged many synonymies within *Ctenus*, which now comprises well over 200 recorded species.

Relationships of the Ctenidae with other spider families are hardly well settled. Since early in their taxonomic history, ctenids have been variously allied to pisaurids (Walckenaer, 1805), clubionids (Simon, 1897a, 1909), sparassids (Bertkau, 1878), lycosids (Homann, 1961, 1971; Thorell, 1892; Keyserling 1876), miturgids (Simon, 1897a), oxyopids (Thorell, 1892; Keyserling, 1876), zorids (Mello-Leitão, 1936; Main, 1954; Petrunkevitch, 1928; Simon, 1909), and zoropsids (Petrunkevitch, 1910; Simon, 1892, 1906).

The family Ctenidae was created by Keyserling in 1876 to include *Ctenus* and three other new genera (*Acanthoctenus*, *Calocteneus*, and *Oligoctenus*). He placed the family in the suborder Citigradae together with the lycosids and oxyopids, from which ctenids were separated by the presence of two tarsal claws, scopulae beneath the tarsi, and three ocular rows arranged in a 2–4–2 pattern (anterior median eyes in a first row, posterior median and anterior lateral eyes in a second row, and posterior lateral eyes alone in a third row).

Currently, the family comprises 38 genera (Platnick, 1997) united by the above characters. All but the last character exhibit high levels of homoplasy, arising independently many times in various spider groups.

The ocular arrangement in 2–4–2 rows occurs also in a few other families. Among these, the following taxa closely resemble the ctenid ocular pattern: *Cycloctenus* Koch, 1878, currently placed in Cycloctenidae; *Senoculus* Taczanowski, 1872, placed in its own family; *Thalassius* Simon, 1885, belonging in Pisauridae; and some zorids. The former three genera are separated from ctenids by having three claws instead of two and by lacking tarsal scopulae and claw tufts. Some Australian zorids belonging to *Argoctenus* L. Koch, 1878 and *Elassoctenus* Simon, 1909, are often identified as ctenids on

the basis of their ocular pattern, and this is also the case for Neotropical zorids (e.g., *Odo* Keyserling, 1887).

Recent studies suggest that the family is polyphyletic. Simon (1892, 1906) placed *Acanthoctenus* in the Zoropsidae, but F.O.P.-Cambridge (1902) later transferred this genus back to the ctenids; however, its position is far from being resolved. Results from the first quantitative, cladistic study of higher-level relationships of lycosoid spiders (Griswold, 1993) showed a closer relationship between *Acanthoctenus* and *Zoropsis*, whereas *Ctenus* and *Phoneutria*, the other two ctenid genera in this analysis, appeared more closely related to *Griswoldia* Dippenaar-Schoeman and Jocqué, 1997 and *Phanotea* Simon, 1896, taxa originally assigned to Miturgidae. On the other hand, results from a second study aimed also at elucidating phylogenetic relationships of lycosoid spiders (Hüber et al., 1993) found *Cupiennius* Simon, 1891 more closely related to both pisaurids and lycosids than to *Phoneutria*. Also, based on behavioral attributes, it has been proposed that *Ancylometes* is more closely related to pisaurids than to ctenids (Merrett, 1988).

Similarities among ctenids, cycloctenids, miturgids, and zorids were already pointed out by Simon (1897a); furthermore, Petrunkevitch (1928: 51) considered zorids to be the "northernmost relatives" of ctenids, which are more commonly found in the southern tropics. To date there are no phylogenetic hypotheses examining the close relationships of all these taxa, but it is clear that the limits of the family are far from being well defined.

TAXONOMIC BACKGROUND

Early attempts to subdivide ctenids into natural groups include that of Simon (1897a). Simon suggested a close relationship between ctenids, clubionids, and sparassids, from which ctenids were distinguished by the eye proportion and arrangement: that is, three rows, with the first one comprising two eyes, relatively large and close together; a second one with four eyes, two medians very large, rounded and convex, and two laterals very small, oval-shaped, oblique, and paler; and a third row situated dorsally with two eyes very large, far apart from each other, and mounted on small tubercles. He pointed out that the eyes form two strongly recurved rows, especially the first one where the anterior lateral eyes move back to the same level as the posterior median eyes; however, the variation of the eyes defined as forming either a procurved or recurved row is seen in Simon's placement of such genera as *Titiotus* Simon, 1897 or *Uliodon* L. Koch, 1873 within his Cteneae: the former one is currently placed in Tengellidae, whereas the latter belongs in Miturgidae, neither of which exhibits the ctenid eye arrangement. This is also the case for other taxa currently assigned to either Ctenidae or Zoridae, in particular *Itatiaya* Mello-Leitão, 1915, *Trujillina* Bryant, 1948, *Odo lycosoides* (Chamberlin, 1916), and most Australian zorid taxa.

Simon placed ctenids as a subfamily of Clubionidae and divided Cteninae into three groups: Cteneae, Acantheae, and Caloctenneae. Despite sharing the ctenid ocular pattern, neither *Acanthoctenus*, *Ancylometes*, nor *Vulsor* Simon, 1888 was included in any of these three groups. Based on the presence of a cribellum, *Acanthoctenus* was placed with *Zoropsis* Simon, 1878 in the Zoropsidae as part of a Cribellatae section. The presence of a third tarsal claw justified placing *Ancylometes* in the Pisauridae. The reduction of tibial ventral spines and the posterior lateral spinnerets with an elongate distal segment indicated a closer relationship between *Vulsor* and *Miturga* Thorell, 1870. Later, Simon (1909) modified this classification by transferring Miturgeae and Zoreae from the Liocraninae to the Cteninae and placing *Vulsor* within the caloctenines.

Other attempts to classify ctenids were presented by Petrunkevitch (1928), Mello-Leitão (1936), and Lehtinen (1967). Both Petrunkevitch and Mello-Leitão proposed some changes to Simon's classification. Lehtinen departed from all these views and suggested rather controversial groupings. Petrunkevitch placed Simon's Zoreae within acantheines and placed *Acanthoctenus* in its own family. On the other hand, Mello-Leitão created the argoctenines to incorporate Zoreae within the ctenids and considered *Vulsor* as a member of this group. Lehtinen revalidated *Viridasius* Simon, 1888 and proposed the viridasines;

this new subfamily did not include *Vulsor*, which was regarded as incertae sedis. Lehtinen suggested other various changes in the composition of ctenines, acantheines, and caloctenines, but they hardly represented natural groupings.

In general, none of the above classifications refers to monophyletic groups, and currently many of Simon's ctenines, as well as members of various subfamilies proposed by later authors, are placed either in the Zoridae, Liocranidae, Miturgidae, or Pisauridae.

Araneomorphae is by far the largest of the three major monophyletic groups currently recognized for the order Araneae (Platnick and Gertsch, 1976). Among them, the Lycosoidea appears to be a natural group based on one morphological character, a grate-shaped tapetum in at least the posterior median eyes (Griswold, 1993; Homann, 1971), which is independently derived in the stiphidiids, being recently moved to a more basal position (Griswold et al., 1999). Lycosoids comprise roughly 3700 species (Coddington and Levi, 1991) distributed in various families, including, among others, the ctenids, lycosids, pisaurids, trechaleids, senoculids, oxyopids, and zoropsids. Lycosoids (Griswold, 1993) are divided into three clades: the "ctenoid complex", the "zoropsoid complex", and the "higher lycosoids".

The zoropsoids include *Acanthoctenus* and *Zoropsis*. This group was first recognized by Simon (1892: 227) on the basis of a shared cribellum, scopulae beneath metatarsi and tarsi, tarsal claw tufts, two tarsal claws, and first and second tibiae with paired long spines resembling those in some zorids or agelenids. In Griswold's (1993) hypothesis, zoropsoids are defined by the presence of dense claw tufts and highly spinose first and second legs, in addition to the presence of a cymbial scopula and a labium length-to-width ratio less than 1.18.

In that analysis (Griswold, 1993), the ctenoid complex included *Devendra* Lehtinen, 1967, *Phanotea*, and *Griswoldia* (originally *Machadonia* Lehtinen, 1967 was used, but that name is preoccupied), genera formerly placed in Miturgidae, and the ctenids, represented by *Ctenus* and *Phoneutria*. The monophyly of this clade was supported by a tegulum with a cup-shaped median apophysis, epigynal lateral lobes with toothlike projections, and a well-defined male tibial crack in all legs—lost in ctenids and independently derived in *Zoropsis*. *Griswoldia* appeared as the sister group of ctenids based on the presence of a broad labium and two or more dorsal spines on the male first tibia.

In Griswold's analysis, the higher lycosoids were supported by evidence provided by the male palp, especially the absence of subtegular and tegular lobes. Two sub clades were recognized, the "stiphidiids" and the "higher lycosoids". In the former, the psechrids were sister to a clade formed by (*Stiphidion* (*Senoculus* + *Oxyopes*)) based on the occurrence of a large spermathecal head (with reversal in *Senoculus*), the sternum extending to coxae IV, a single row of tarsal trichobotria (also reverting in *Senoculus*), a shallow trochanteral notch, and the loss of tarsal scopulae. Although *Stiphidion* is no longer a member of Lycosoidea, *Psechrus* still appears to be the most basal taxon of the higher lycosoids (Griswold et al., 1999).

Among the higher lycosoids, *Uliodon*, at times placed within ctenids but now listed in miturgids, was sister to a clade formed by pisaurids, trechaleids, and lycosids; this sister-group relationship was supported by a membranous cuticle connecting the embolus to the tegulum, a lobate process at the embolic base, the loss of cribellum and calamistrum, and labium length-to-width ratio less than 1.18. The position of *Uliodon* is still controversial and to date there are no studies including *Miturga* that test this hypothesis.

F.O.P.-Cambridge (1897a) considered *Cupiennius* an odd ctenid taxon for having a third tarsal claw and also for carrying the egg sac with the spinnerets, a feature typical of lycosid spiders. This genus is one of the most common spiders in the Neotropics; its behavior has encouraged studies on ecology (Barth et al., 1988; Barth and Schmitt, 1991; Melchers, 1963), electrophysiology (Barth and Holler, 1999; Schmid, 1998; Barth et al., 1993; Land and Barth, 1992), and anatomical ultrastructure (Gorb and Barth, 1996; Seyfarth, 1985; Barth and Libera, 1970), among many others. Although *Cupiennius* is already well diagnosed (Barth and Cordes, 1998; Brescovit and Eickstedt, 1995; Lachmuth et

al., 1994), its familial position is still not clarified.

Hüber et al. (1993) sequenced the 16S mtDNA for one species of *Phoneutria* and three species of *Cupiennius* as exemplars for Ctenidae, along with two species of Pisauridae, one Lycosidae, one Clubionidae, and one Liphistiidae. No intraspecific variation was found and the interspecific variation within *Cupiennius* was very low (3–4%). Some trees varied slightly in the position of *Cupiennius* regarding the lycosid and pisaurids but none found a sister-group relationship between *Phoneutria* and *Cupiennius*; these results argued against the monophyly of ctenids.

Piel (personal commun., 1998) using the Harvard Museum of Comparative Zoology tree database, replicated their analysis and found most parsimonious trees supporting the monophyly of lycosoids (Griswold, 1993). He also replicated Griswold's data with the inclusion of *Cupiennius* and his results supported the hypothesis of Hüber et al. (1993) in showing this genus more closely related to the higher lycosoids than to the ctenids. Eight characters supported this relationship, but only one was in substantial conflict with typical ctenids; that is, the absence of subtegular/tegular interlocking lobes (character 6 in Griswold, 1993), a putative synapomorphy for higher lycosoids.

Ancylometes is a genus currently placed in the Pisauridae (Merrett, 1988), based on the presence of a third tarsal claw, absence of tarsal scopulae, and the construction of a nursery web; the habitus in some species much resembles that of species belonging to *Dolomedes* and *Thalassius*, and the male palp has a strongly sclerotized conductor like that found in some pisaurids. Lehtinen (1967) transferred some pisaurids, among them *Thalassius*, to the Ctenidae and created the thalassiines, which include also *Ancylometes* and *Cupiennius*. Sierwald's studies (1987, 1990) provided several synapomorphies supporting the monophyly of *Thalassius*, its position within the Pisauridae, and its close relationship to *Dolomedes*. Additionally, based on the ctenid ocular pattern, a similar dorsal spination on both male and female metatarsi, and the reduction of the median tarsal claw, Sierwald (1987: 63–64) suggested that both *Cupiennius* and *Ancylometes* may belong in the Ctenidae.

The position of Ctenidae among Lycosoidea is still unresolved. Homoplasies obscure the relationships of the families within each complex, making them a matter of controversy, particularly when dealing with the ctenoid and zoropsoid spiders. Overall, the family Ctenidae has never been the subject of a strict cladistic analysis, and herein I test its monophyly and higher-level relationships in order to provide a framework for improving the classification of this group.

MATERIALS AND METHODS

A total of 98 terminals representing 16 families and three genera incertae sedis were scored in a matrix with 146 characters (appendix 2). All but six characters came from various morphological systems; the others are behavioral attributes. Polarity for character states was determined by rooting the tree with an outgroup (Nixon and Carpenter, 1993). The outgroup (table 1) is composed of a wide array of taxa once thought to belong in the ctenids or to be their closest relatives. The ingroup (table 2) comprises almost all the genera currently listed under Ctenidae; those not included are either those known from their type specimens, which are not available (e.g., *Paravulsor* Mello-Leitão, 1922, *Pseudoctenus* Caporiacco, 1949, and *Trogloctenus* Lessert, 1935); or those from misplaced taxa (e.g., *Wiedenmeyeria* Schenkel, 1953 [a juvenile *Acanthoctenus*, personal obs.] and two Australian taxa congeneric with *Argoctenus*, personal obs.]). This broad taxonomic sampling should result in a stricter test of the monophyly of ctenids as well as place in a better context some characters traditionally used for defining the family.

Based on the most recent cladistic hypothesis for entelegyne relationships (Griswold et al., 1999), the nicodamid *Megadictyna thillenii* Dahl was chosen to root the tree. This further tests the relationships between amaurobiids and ctenids and helps determine the position of taxa that have never been subjected to cladistic analyses, such as cycloctenids and zorids. Although ongoing studies for South American and Australian zorids involve cladistic analyses, the results are not

yet available and therefore the position of these groups is still uncertain.

The matrix (appendix 2) had 88.86% real values; unknown data represented 4.72% and nonapplicable data 6.40%. Following Platnick et al. (1991a), unknown and nonapplicable data are represented as "?" and "–", respectively, in order to facilitate the examination of character transformation and clade support. Multistate characters were coded as nonadditive, because I was not able to accurately determine character state adjacencies or to produce enough information to justify a particular series of transformations. Multistate characters were used primarily to distinguish terminal taxa that were otherwise redundant in the current matrix.

Many characters were taken from various literature sources, including phylogenetic studies (Griswold et al., 1999; Griswold, 1993; Platnick et al., 1991b; Sierwald 1989, 1990), taxonomic revisions (Carico, 1973, 1993; Sierwald, 1987, 1993), or general treatises (Petrunkevitch, 1933; Simon, 1897a); all of them were checked in a broad set of ctenid species.

DADA (version 1.3, Nixon; 1995) was used to construct the matrix for running cladistic analyses based on parsimony (Farris 1983; Farris et al., 1996; Goloboff, 1993, 1994; Nixon, 1999). Searches for the most parsimonious trees were carried out with implied weights using Pee-Wee (version 3.0; Goloboff, 1999b). A search for a tree with the best fit was routinely performed with the default setting, amb-, in order to allow only unambiguous support. All available values of the concavity function (K = 1–6) for weighting homoplasy were used. Wagner trees were created by invoking multiple random taxa additions followed by tree bisection/reconnection branch swapping. A total of 2000 replications, holding 50 trees at each iteration, were followed by additional TBR swapping (max*).

The matrix was also analyzed with the parsimony ratchet (Nixon, 1998) as implemented in both Pee-Wee (K = 1–6) and NONA. The final trees were generated by using the commands "hold1000; hold/1; nix* 30 300" but various combinations were routinely tested for finding additional islands of trees. The ratchet will reweight a subset of the characters, create a random-addition-sequence Wagner tree, perform branch swapping using TBR, reverse the weights back, perform another round of TBR until it reaches 30 iterations and, then recreate a Wagner tree and repeat the cycle in order to complete 300 replications (Nixon, 2000; Goloboff, 1999b).

For comparison, analyses with equal weights were conducted with Hennig86 "mh*;bb*;" commands and NONA (version 2.0; Goloboff, 1999a) with the same commands as Pee-Wee. All equally weighted searches were subjected to successive character weighting (Farris, 1969; Carpenter, 1988). The new weights were based either on the rescaled CI (Hennig86) or the CI (NONA). Results from all searching strategies were routinely summarized by consensus trees ("nelsen").

All resulting trees were submitted to Clados (Nixon, 1998) or WinClada, BETA version 0.9 (Nixon, 1999), for character optimization, tree drawing, and statistics; the latter two were complemented with outputs from Pee-Wee, which also provided a list of unambiguous changes occurring in all of the most parsimonious trees ("apo-*").

Branch support was calculated by two approaches (Oxelman et al., 1999: 176): (1) Bremer support (Bremer, 1988, 1994), being more sensitive to quantitative differences among clades, and (2) parsimony jackknife (Farris et al., 1996), a resampling method more sensitive to the structure in the entire data matrix. Bremer support values measure the number of extra steps required to collapse a group by taking into account a set of less parsimonious trees. In order to better estimate these values, a batch of suboptimal trees starting with bs1 to bs 120 (1 degree of fitness from 1 to 15 and 5 degrees from there to the end) were generated. By contrast, parsimony jackknife measures the sensitivity of data to removal of characters with a probability of 0.36; clades that are not supported by many strong characters end up having frequencies equal to or lower than 50% and therefore are eliminated in the final majority consensus tree.

Exemplar Species

All taxonomic changes in this study were proposed after examination of the corre-

sponding holotypes, new material, and the results of the cladistic analysis. Voucher specimens used as terminals for this study have been appropriately labelled and deposited at the AMNH unless otherwise indicated.

Outgroup Taxa

In view of the wide variety of taxa thought to be ctenids or closely related to them, many genera placed in various families were examined (table 1). Terminals for the final matrix are species represented by at least one male and one female from the same locality, when possible; if one of them was not available, the information was taken from the literature or remains unknown.

Redundant species for the current dataset were removed, and therefore some genera are represented by a single terminal (e.g., *Dolomedes* spp.). When dubious clusterings occurred, a second or third species belonging

TABLE 1
Summary List of Outgroup Taxa Chosen for Cladistic Analysis
Vouchers are at AMNH unless otherwise indicated.

1. **Nicodamidae**
   - *Megadictyna thillenii* Dahl, 1906
2. **Amaurobiidae**
   - *Amaurobius ferox* (Walckenaer, 1830)
   - *Pimus napa* Leech, 1972
3. **Clubionidae**
   - *Clubiona canadensis* Emerton, 1889
   - *Elaver texana* (Gertsch, 1933)
4. **Cycloctenidae**
   - *Cycloctenus* cf. *flavus* Hickman, 1981
   - *Cycloctenus* cf. *flaviceps* Koch, 1871
   - *Cycloctenus westlandicus* Forster, 1964
5. **Liocranidae**
   - *Liocranum rupicola* (Walckenaer, 1830)
6. **Lycosidae**
   - *Hogna frondicola* (Emerton, 1885)
   - *Aglaoctenus castaneus* (Mello-Leitão, 1938)
7. **Miturgidae**
   - Eutichurinae
     - *Eutichurus lizeri* Mello-Leitão, 1938
     - *Strotarchus piscatorius* (Hentz, 1847)
   - Miturginae
     - *Miturga lineata* Thorell, 1870 (QMS)
     - *Teminius affinis* Banks, 1897
   - Uliodoninae
     - *Uliodon tarantulinus* (L. Koch, 1873) (AMNH/QMS-female)
8. **Oxyopidae**
   - *Peucetia viridans* (Hentz, 1832)
9. **Pisauridae**
   - *Ancylometes bogotensis* (Keyserling, 1877)
   - *Dolomedes fimbriatus* (Clerck, 1757)
   - *Dolomedes* tenebrosus Hentz, 1844
   - *Dolomedes triton* (Walckenaer, 1837)
   - *Thalassius rubromaculatus* Thorell, 1899
   - *Thalassius spinosissimus* (Karsch, 1879)
10. **Psechridae**
    - *Psechrus sinensis* Berland & Berland, 1914
11. **Senoculidae**
    - *Senoculus* sp. [Sen 1, Peru: Rio Samiria]
    - *Senoculus* cf. *gracilis* (Keyserling, 1879)
12. **Tengellidae**
    - *Anachemmis sober* Chamberlin, 1919
    - *Liocranoides unicolor* Keyserling, 1881
    - *Tengella* cf. *radiata* (Kulczynski, 1909), female
    - *Tengella albolineata* (F.O.Pickard-Cambridge, 1902), male
    - *Titiotus* sp.
13. **Trechaleidae**
    - *Trechalea connexa* (O. Pickard-Cambridge, 1898)
14. **Zoridae**
    - *Argoctenus* cf. *davisi* Rainbow, 1898
    - *Diallomus* ca. *speciosus* Simon, 1897 (CDC)
    - *Elassoctenus* ca. *harpax* (Simon, 1909) (QMS)
    - *Hestimodema* cf. *latevittata* Simon, 1909
    - *Neoctenus* ca. *comosus* Simon, 1897
    - *Odo* cf. *agilis* Simon, 1897
    - *Odo* sp. [Chile]
    - *Odo* ca. *lycosoides* (Chamberlin, 1916) (MACN)
    - *Odo* cf. *obscurus* Mello-Leitão, 1936
    - *Odo patricius* Simon, 1900 [ca. *Xenoctenus marmoratus* Mello-Leitão, 1941]
    - *Zora spinimana* (Sundevall, 1833)
15. **Zoropsidae**
    - *Zoropsis rufipes* (Lucas, 1838)
16. **Zorocratidae**
    - *Raecius* sp. (CAS)
    - *Uduba* sp. (CAS)
    - *Zorocrates* cf. *guerrerensis* Gertsch & Davis, 1940
    - *Zorodictyna* sp.
17. **Incertae sedis**
    - Machadoninae (ex Miturgidae)
      - *Griswoldia acaenata* (Griswold, 1991) (CAS)
      - *Phanotea digitata* Griswold, 1994 (MRAC)
      - Chile 1 [Tregualemu]

to a monophyletic genus/group was incorporated in order to facilitate the introduction of characters otherwise autapomorphic.

Ingroup Taxa

A broad sample of ctenid species, representing nearly all genera currently recognized, were chosen as terminals for this study (table 2). Numerous species from a broad geographic range of the Ctenidae were examined for a better grasp of morphological variation at generic and intraspecific levels as well as the phylogenetic diversity of the family. The exemplars chosen represent all ctenid subfamilies recognized at present: acantheines, acanthoctenines, caloctenines, ctenines, phoneutriines, and viridasines.

Since most ctenid genera currently recognized appear to comprise small groups well characterized by a unique combination of genitalic and morphological characters, a single species is assumed to represent a genus. The inclusion of two or more species of a single genus often resulted in redundancy of data for all the characters scored in the data matrix. However, two or more species of a single genus were selected to account for a wide variation in some of the characters used. Selection of the terminals was based on availability of both males and females of the same species.

In the case of the type genus, *Ctenus*, which has served as a taxonomic wastebasket since very early in ctenid taxonomic history, several species were examined. This genus includes more than 200 nominal species from throughout the world, but for practical reasons only a few species from various geographic regions were finally chosen, especially those with features that could provide some evidence supporting the monophyly of ctenines or shed some light on the relationships among them.

On the other hand, *Ctenus coxalis* F.O.P.-Cambridge is regarded as congeneric with *Isoctenus eupalaestrus* Mello-Leitão and *I. janeirus* (Walckenaer) and was selected to represent the latter genus in the cladistic analysis. An in-depth revisionary work, necessary for testing the monophyly of *Isoctenus*, is in progress (Brescovit and Simó, personal commun.).

Specimen Examination

Specimens were examined following standard procedures for spiders. Male pedipalps were expanded by alternately immersing them in distilled water and in a weak KOH solution until expansion stopped (Griswold, 1991). The epigynum was excised from the abdomen and placed in a proteolytic solution until the soft tissue was completely removed (Sierwald, 1990; Coddington, 1986); after that, it was transferred to 75% ethanol for observation and drawing. Prior to examination under the compound microscope, both male and female genitalia were temporarily mounted on depression slides with 85% lactic acid.

When available material was at hand, tracheae were observed in at least one adult female of each genus; otherwise, immature specimens were examined. The dorsal cuticle of the abdomen was removed and the abdomen transferred to saturated KOH, boiled to remove all soft tissue, rinsed in distilled water, and transferred to 75% ethanol for examination with a stereomicroscope (Griswold, 1991).

For scanning electron microscopy (SEM), structures were ultrasonically cleaned, left overnight in absolute ethanol, either critical point or air dried, mounted, and sputter-coated with gold-palladium. Spinnerets were routinely examined under the stereomicroscope, and when more than two adult males and females were available, they were prepared for SEM examination (Coddington, 1989).

When not visible, the tapeta were examined under a stereomicroscope either by immersing the cephalothorax in lactic acid overnight or by dissecting the eyes (Griswold, 1991). For the latter method, adult females were examined only when enough specimens were available; otherwise, immature specimens were prepared.

For this study a Wild M-5 stereomicroscope with an eyepiece micrometer was employed. Illustrations were made with a Wild 1.25× drawing tube. A compound microscope with either a camera lucida or a photographic camera was used to examine and draw further details of the male and female genitalia.

TABLE 2

List of Ctenid Species Selected as Terminals for Cladistic Analysis

Male and female vouchers are deposited at AMNH unless otherwise indicated.

Taxon	Collection	Distribution
Acantheinae		
Acantheis n. sp.		Vietnam
Africactenus guineensis (Simon, 1897)	MNHN	Sierra Leone
Enoploctenus cyclothorax (Bertkau, 1880)	MNHN-male/MCN-female	Brazil
Petaloctenus bossema Jocqué & Steyn, 1997	MRAC	Ivory Coast
Acanthocteninae		
Acanthoctenus spiniger Keyserling, 1877		Mexico
Nothroctenus cf. *marshii* (F.O.P.-C., 1897)	MACN	Argentina
Viracucha andicola (Simon, 1906)	IB	Brazil
Calocteninae		
Anahita isaloensis Ono, 1993	MRAC	Madagascar
Anahita punctulata (Hentz, 1844)		USA
Anahita blandini Benoit, 1977	MRAC	Ivory Coast
Anahita n. sp.		New Caledonia
A polania segmentata Simon, 1898	MRAC	Seychelles Is.
Caloctenus n. sp.	MUSM	Peru (Oxapampa)
Caloctenus gracilitarsis Simon, 1897	MNHN	Venezuela
Gephyroctenus cf. *philodromoides* M.-L., 1936		Peru
Trujillina isolata (Bryant, 1942)		Puerto Rico
Trujillina spinipes Bryant, 1948		Dominican Republic
Madagascar 30	CAS	Madagascar
Cteninae		
Amauropelma Raven et al. 2001 (=Australia 1)	QLM	Australia
Lombok	CDC	Indonesia
Asthenoctenus borelli Simon, 1897	MUSM	Argentina
Celaetycheus cabriolatus Franganillo, 1930	MCZ	Puerto Rico
Celaetycheus ca. *flavostriatus* Simon, 1897	IB	Brazil
Centroctenus ocelliventer (Strand, 1909)		Colombia
Ctenus amanensis Strand, 1907	ZMC	Tanzania
Ctenus hibernalis Hentz, 1844		USA
Ctenus indicus Gravely, 1931	JMC	Nepal
Ctenus maculisternis Strand, 1909		Peru
Ctenus miserabilis Strand, 1916		Ecuador
Ctenus mitchelli Gertsch, 1971		Mexico
Ctenus narashinai Patel & Reddy, 1988	ZMC	India
Ctenus villasboasi Mello-Leitão, 1949		Peru
Cupiennius ca. *celerrimus* Simon, 1891		Peru
Isoctenus coxalis (F.O.P.-Cambridge, 1902)	MCN-male 2583/female 20614	Brazil
Leptoctenus ca. *agalenoides* L. Koch, 1878	QLM	Australia
Leptoctenus byrrhus Simon, 1888		USA
Oligoctenus ornatus (Keyserling, 1876)	MCZ-male/AMNH-female	Brazil
Oligoctenus ca. *medius* (Keyserling, 1891)		Panama
Thoriosa ca. *spadicea* (Simon, 1910)	CAS	São Tomé
Peru 1		Peru
Tanzania 1	ZMC	Tanzania
Vietnam 1		Vietnam
Phoneutriinae		
Phoneutria boliviensis (F.O.P.-Cambridge, 1897)		Peru

TABLE 2
(Continued)

Taxon	Collection	Distribution
Viridasiinae		
Madagascar 2	CAS	Madagascar
Madagascar 25	CAS	Madagascar
Viridasius fasciatus (Lenz, 1886)	MNHN	Madagascar
Viridasius pulchripes Simon, 1889	MNHN	Madagascar
Vulsor ca. *bidens* Simon, 1889	CAS	Madagascar
Incertae sedis		
Janusia muiri Gray, 1973	WAM	Australia
Australia 15[a]	KS	Australia
Brazil 1	MCN 16872	Brazil

[a]*Bengalla bertmaini* Gray and Thompson, 2001.

Collections Examined

AMNH American Museum of Natural History, New York (N. Platnick)
BMNH Natural History Museum, London (J. Margerison, P. Hillyard)
CAS California Academy of Sciences, San Francisco (C. Griswold)
CDC C. Deeleman-Reinhold, Ossendrecht, Netherlands
FMNH Field Museum of Natural History, Chicago (P.P. Parrillo)
IB Instituto Butantan, São Paulo (A.D. Brescovit)
ICC Instituto de Ciencias de Cuba, Habana (A. Pérez Gonzáles)
IFML Instituto y Fundacion Miguel Lillo, Tucumán (P. Goloboff)
JAM J.A. Murphy collection, London, England
JMC Jochen Martens collection, Mainz, Germany
KS Australian Museum, Sydney (M. Gray)
MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (C. Sciocia)
MCN Museu de Ciencias Naturais, Porto Alegre (E. Buckup)
MCP Pontificia Universidade Catolica do Rio Grande do Sul, Porto Alegre (A.A. Lise)
MCZ Museum of Comparative Zoology, Harvard University, Cambridge (L. Leibensperger, H.W. Levi)
MHNCI Museu de Historia Natural "Capão da Imbuia", Curitiba (R. Pinto da Rocha)
MNHB Museum für Naturkunde, Berlin (P. Moritz; J. Dunlop)
MNHN Muséum National d'Histoire Naturelle, Paris (C. Rollard)
MRAC Musée Royal de L'Afrique Centrale, Tervuren (R. Jocqué)
MUSM Museo de Historia Natural, Lima (G. Lamas, D. Silva)
MZS Museo Zoologico de "La Specola", Florence (L. Bartolozzi)
NHMB Naturhistorisches Museum, Basel (C. Stocker)
PSC Peter Schwendinger Collection, Innsbruck, Austria
QM Queensland Museum, Brisbane (R.R. Raven)
SMF Senckenberg Museum, Frankfurt (M. Grasshoff)
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C. (J. Coddington)
WAM Western Australian Museum, Perth (M.S. Harvey)
ZMK Zoological Museum, University of Copenhagen (N. Scharff)

CLADISTIC ANALYSIS

Supporting Evidence

The results of all analyses show several suprageneric taxa supported by rather low Bremer support values. On average, the values from NONA (NBS) and Pee-Wee (PBS) were equivalent in the degree of support of similar clades (i.e., values were either high or low regarding other clades in the same tree). Some of the monophyletic groups found by both equal and implied weighting are the following: cycloctenids (NBS = 15,

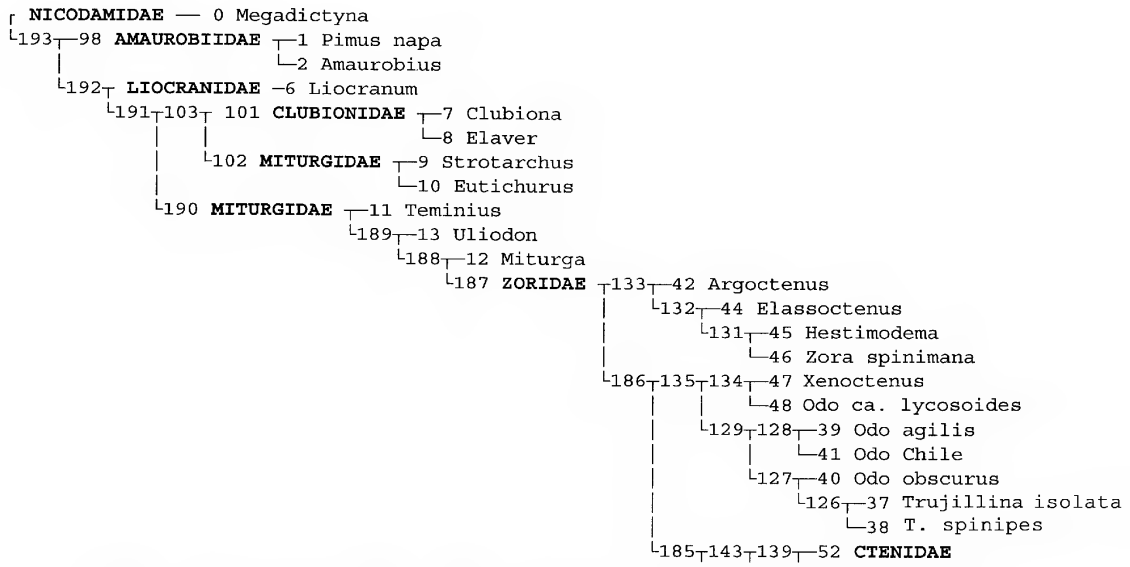

Fig. 1a. Consensus tree of >1000 most parsimonious trees from equal weighting.

PBS = 10.4), *Clubiona* + *Eutichurus* (NBS = 4, PBS = 2), *Peucetia* + *Senoculus* (NBS = 13, PBS = 1.8), senoculids (NBS = 21, PBS = 2.4), *Thalassius* + *Dolomedes* (NBS = 22, PBS = 8.4), *Titiotus* + *Anachemmis* (NBS = 14, PBS = 1.9), Chile 1 + *Phanotea* (NBS = 17, PBS = 1.1), *Zoropsis* + *Zorodictyna* (NBS = 13, PBS = 1.0), *Xenoctenus* + *Odo* (NBS = 11, PBS = 0.4), *Argoctenus* + *Hestimodema* (NBS = 11, PBS = 5.3), viridasines (NBS = 17, PBS = 1.2), acanthoctenines (NBS = 16, PBS = 5.9), caloctenines (NBS = 16, PBS = 0.1), *Thoriosa* + Lombok (NBS = 20, PBS = 1.6).

In general, most characters require subsequent reversals or independent origins several times. This is reflected (1) in that several searching strategies produced different sets of trees, (2) in higher groups supported by low Bremer values or no support at all, and (3) in few groupings at suprageneric levels resolved by parsimony jackknife.

The statistics for the 146 characters used in this analysis and their behavior as optimized on the preferred tree are shown in appendix 1. The chosen working hypothesis is 1 of 591 most parsimonious trees generated by implied weighting (K = 6, parsimony ratchet). A description of each character is presented in appendix 1.

Equal Weighting Analysis

Heuristic searching in Hennig 86 yielded 652 trees (overflow) of length (L) 792, consistency index (CI) of 0.33, and retention index (RI) of 0.68. Successive weighting stabilized after five rounds and resulted in 653 trees (L =1652, CI = 0.75, RI = 0.88), none of which were members of the original set of most parsimonious trees (L = 829–834).

Analyses using NONA yielded 118 trees; however, additional TBR swapping found more than 1000 most parsimonious trees (L = 790, CI = 0.33, RI = 0.68); these trees are summarized in figure 1a–c. Successive weighting stabilized on iteration 2 and resulted in five trees of 26,509 steps (L = 804, CI = 0.33, RI = 0.67).

Although some of the relationships portrayed in the preferred hypothesis were also supported by equal weighting analyses (e.g., the sister-group relationship between *Clubiona* and *Eutichurus*), in general, hypotheses of homology were not well interpreted with equal weighting. It appears that the occurrence of highly homoplasious characters led to unreliable character optimizations and therefore to the recognition of very odd clusterings involving groups otherwise monophyletic. For example, figure 1b and 1c shows that ctenids are polyphyletic due to the

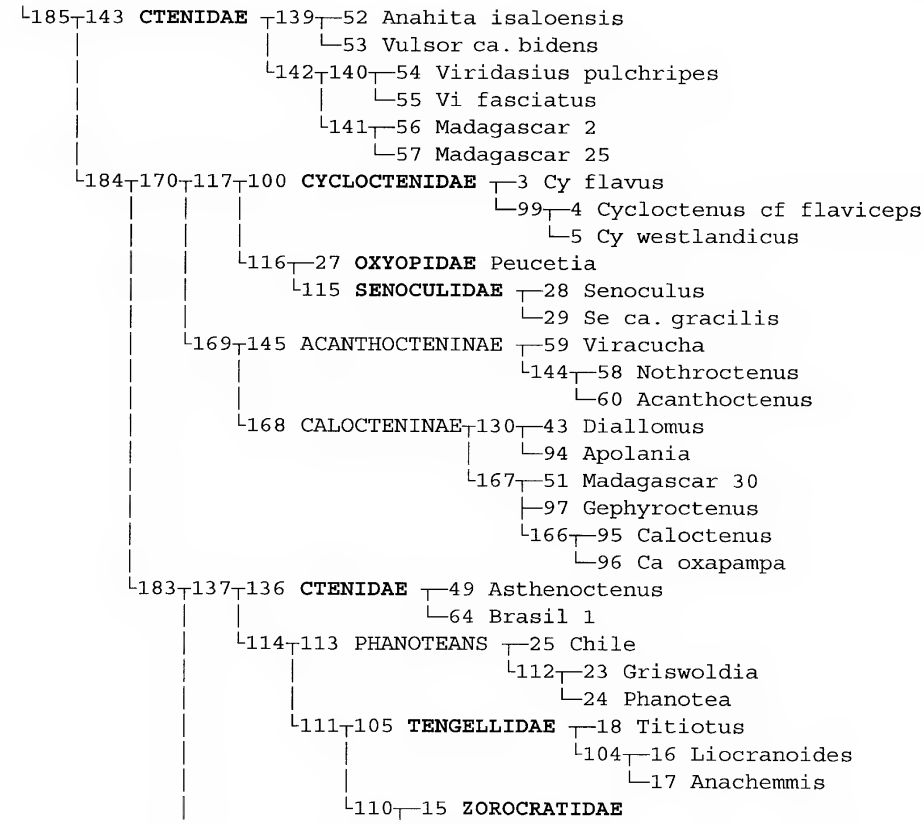

Fig. 1b.

inclusion of such taxa as cycloctenids, oxyopids, and senoculids on one branch and a combination of miturgids, tengellids, and zoropsids plus the higher lycosoids in two other (different) branches.

Parsimony Weighting

This method was preferred as a better approach to dealing with the high levels of homoplasy provided by the characters traditionally used in ctenid classification. In general, a tree-searching protocol invoking the command "mult* 2000" yielded the same most parsimonious trees as those found with the ratchet (in addition to several other suboptimal trees).

Table 3 shows the results of various searching strategies using the parsimony ratchet as implemented in Pee-Wee. The most parsimonious trees (K = 1–6) differ in the placement of the clades (*Titiotus* + *Anachemmis*) and (*Xenoctenus* + *Odo*), as well as in the interrelationships of such clades as the "tengelloids" and "lycosoids", especially in the relationships within ctenids, particularly those among ctenines.

Consensus trees from various searching strategies (K = 1–6) showed amaurobiids (jak = 82%, BS = 1.4) branching off right after the root (fig. 2a). These results agreed with a hypothesis proposing a basal position of the amaurobiid spiders relative to the lycosoids and their kin (Griswold et al., 1999). Although most analyses (K =1–3, 5–6) found cycloctenids (jak = 100%, BS = 10.4) as the next most basal group, analyses with K = 4 indicated that cycloctenids are sister to a group formed by oxyopids and senoculids; in turn, this entire clade clusters within ctenids supported by the occurrence of three ocular rows instead of two (char. 84). When character 84 is deactivated, the resulting trees at K = 4 were almost identical to those found at K = 5–6: they differed only in the position

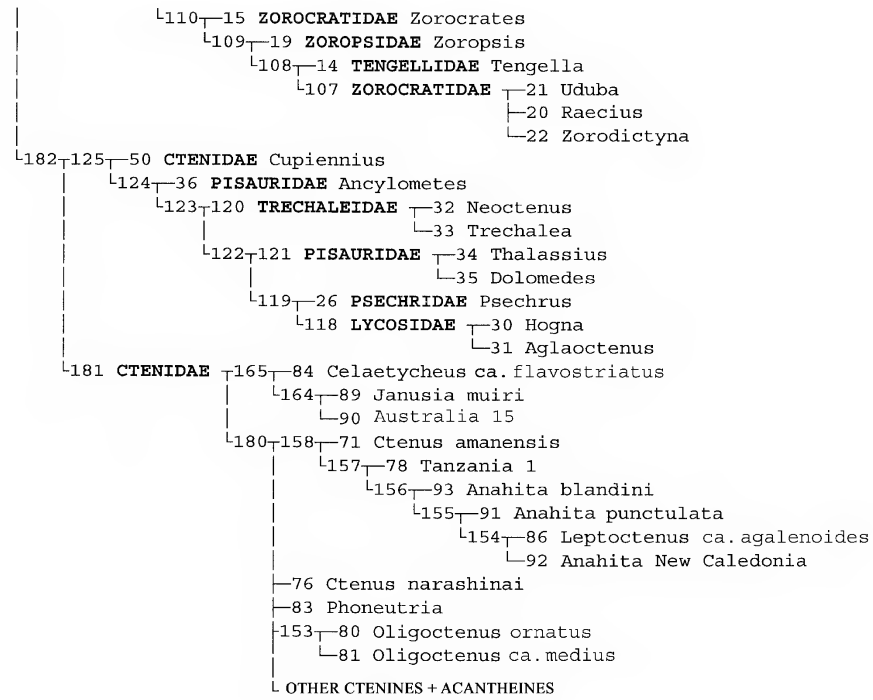

Fig. 1c.

of the *Xenoctenus* + *Odo* clade and some arrangements within ctenines.

Alternative hypotheses showing a sister-group relationship between cycloctenids and all of the remaining taxa (fig. 2a) are primarily supported by the loss of paracribellar spigots (char. 135), as well as by the presence of three dorsal spines on femur I (char. 96), loss of calamistrum (char. 102) (reversed in the remaining cribellates), and the attachment of the egg sac onto a substrate other than a web (char. 146).

Based on the presence of precoxal sclerites (char. 77), all resulting trees show a monophyletic clade (jak = 62%, BS = 0.3) comprised of liocranids, clubionids, and the miturgids *Strotarchus* and *Eutichurus* (fig. 2a). Previous analyses with character 77 deactivated found trees with *Strotarchus* and *Eutichurus* basal to (*Miturga* + *Zora*). In the current matrix, even when this character was deactivated, these four taxa did not cluster together. Both *Strotarchus* and *Eutichurus* lack cylindrical gland spigots (Ramirez et al.,

TABLE 3

Resulting Trees from Implied Weighting

MPT = most parsimonious trees after collapsing unsupported nodes in Winclada. K = concavity function.

K	Trees	MPT	FIT	Length	CI	RI
1	>1000	21	812.6	823–829	32	66
2	186	12	905.9	821–823	32	66
3	20	12	971.9	818	32	66
4	54	24	1022	809	32	67
5	>1000	27	1059.8	814–816	32	66
6	591	8	1092.6	813–817	32	66–67

1997: 44; Platnick et al., 1991: 2), whereas *Miturga lineata* has at least three cylindrical gland spigots in the posterior median spinnerets (personal obs.). In any case, the slender elongate distal segment of the posterior lateral spinnerets, traditionally a diagnostic character for miturgids, required at least three independent derivations.

A sister-group relationship between *Strotarchus* + *Eutichurus* and the clubionids is based on the absence of cylindrical spigots (char. 138) and a truncated female palpal tarsus (char. 118). Although the position of *Liocranum* + *Clubiona* varies according to the settings of "K", this clade appears to be the sister group of a more inclusive group, the grate-shaped tapetum clade, comprising the families Psechridae, Lycosidae, Tengellidae, Zorocratidae, Miturgidae, and Ctenidae (GST clade in fig. 3). Among the unambiguous changes supporting this relationship are the occurrence of two or more tarsal trichobothrial rows (char. 106; although some cycloctenids may have two rows instead of a single one) and the ALS spigot cuticle with longitudinal ridges (char. 129).

Depending on the settings of the "K" function, the next clade would be a paraphyletic group comprising the higher lycosoids (Griswold, 1993) (K = 1–4) or a monophyletic group which I am calling the "GST" clade to facilitate my discussion (K = 5–6). The latter hypothesis corresponds to the fittest trees according to the data on hand.

The trees found at K = 5 differ from those at K = 6 in the position of two clades: (1) *Peucetia* + *Senoculus* basal to (true lycosoids + zorocratids (ctenoids)) and (2) *Xenoctenus* + *Odo* sister to the ctenids.

At a concavity function weighting less strongly against homoplasy (K = 6), the ratchet found 169 trees of fit 1092.6 (L = 813–818, CI = 0.32, RI = 0.67). More exhaustive TBR swapping discovered new islands of most parsimonious trees (591 trees). These trees differ from the preferred hypothesis in various arrangements within Ctenidae as it is shown in the consensus tree (fig. 2a, b).

For the current dataset, the trees generated at K = 6 are regarded as the most parsimonious explanation (i.e., shortest tree length and highest fit) of the phylogenetic relationships among all of the examined taxa. As a working hypothesis for examining the monophyly of ctenids and their higher-level relationships, I chose one of these most parsimonious trees. For selecting a preferred tree out of 591 most parsimonious trees, all unsupported nodes were collapsed and only the shortest trees were kept. A further selection was based on (1) the position of the acanthoctenines (basal to both acantheines and caloctenines), (2) the most parsimonious optimization for the appearance of a cup-shaped median apophysis (char. 47), and (3) the most parsimonious optimization of the epigynal median sector modified as a sclerotized, smooth plate (char. 55). Only eight trees fit these constraints, and the preferred tree (figs. 3–11) was finally chosen at random, because the differences among the eight are concentrated in the relationships within the ctenines. Undoubtedly, a set of stronger characters as well as a better sampling of the ctenine spiders will help to improve upon this preliminary attempt for elucidating the higher-level relationships of the ctenid spiders.

HIGHER-LEVEL RELATIONSHIPS

This study corroborated the sister-group relationship between amaurobiids and a clade formed by lycosoids and their kin (Griswold et al., 1999); in this latter clade, cycloctenids are basal to both dionychans (liocranids + clubionids) and the GST clade (fig. 3).

The evidence for the GST clade (fig. 4) is primarily based on the presence of a grate-shaped tapetum in the posterior median eyes (char. 90), although it requires four reversals to a canoe-shaped tapetum in tengellids + zorocratids, *Teminius*, and the *Odo* clade. Additional evidence for the GST clade includes: the loss of cymbial trichobothria (char. 19), reversed at least once within the ctenoids; the occurrence of epigynal median and lateral foldings (char. 52), reversed to a single fold in some ctenoids; a divided chilum (char. 71), reversed at least three times within true lycosoids and ctenoids, and lost in a few other ctenoids; and at least two or three rows of metatarsal trichobothria (char. 108), reversed to a single row in some true lycosoids and ctenoids.

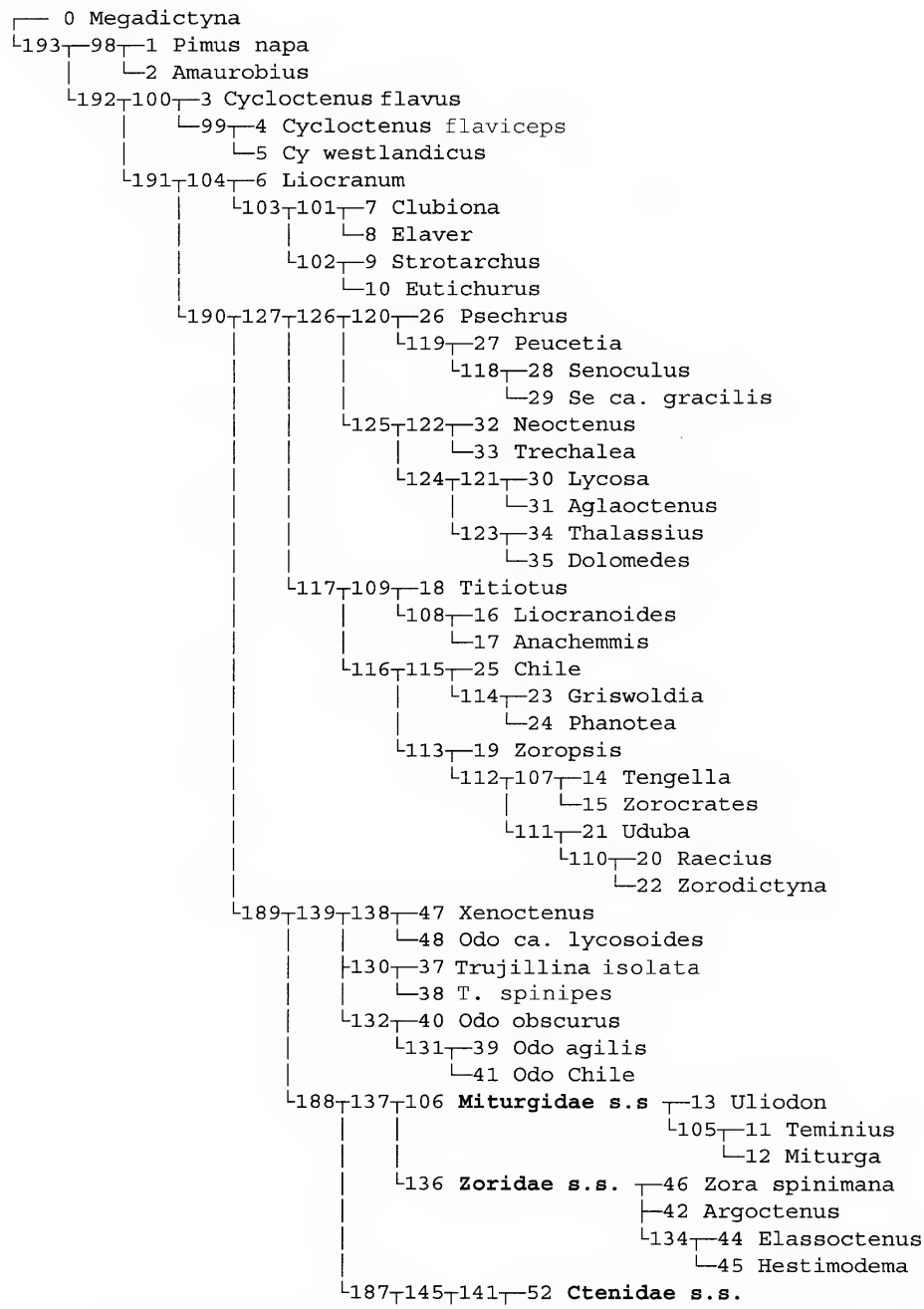

Fig. 2a. Consensus tree of 591 trees from implied weighting.

The GST clade consists of at least three major groups: the true lycosoids, tengelloids, and ctenoids. True lycosoids (fig. 5) correspond to the so-called higher lycosoids (Griswold, 1993) and consist of six families: Psechridae, Oxyopidae, Senoculidae, Pisauridae, Lycosidae, and Trechaleidae. Psechrids branch out first as sister to oxyopids + senoculids and this relationship is supported primarily by the loss of the retolateral tibial apophysis (char. 12), a broad sternum extending between coxae IV (char. 76), and tar-

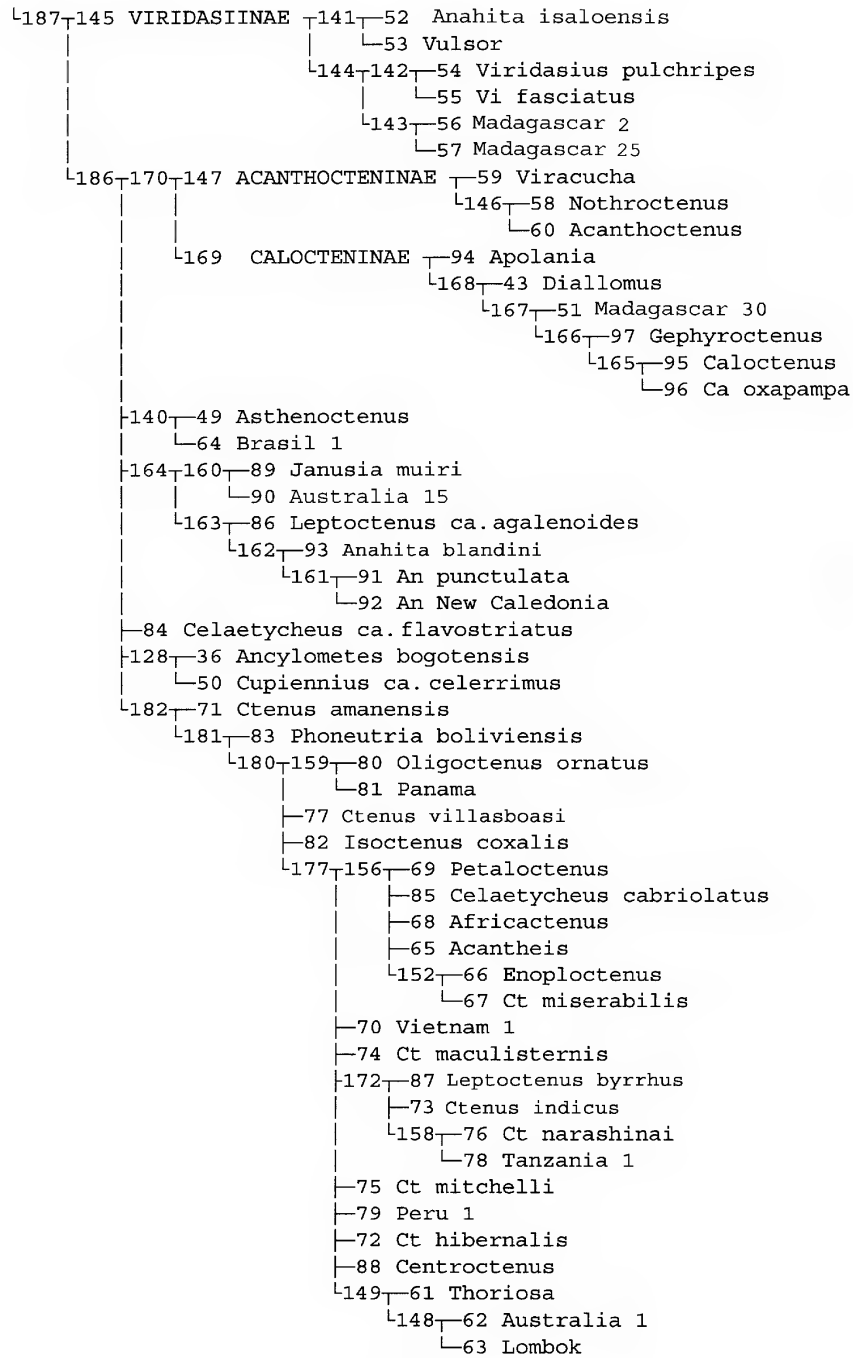

Fig. 2b.

si slightly bent (char. 116), albeit reversed in oxyopids. The relationship (jak = 90%, BS = 1.8) between *Peucetia* and *Senoculus* is primarily based on a rather distinctive, lobate conductor (char. 43) and the absence of a chilum (char. 70).

In turn, the psechrids + senoculids clade is sister to a clade consisting of trechaleids,

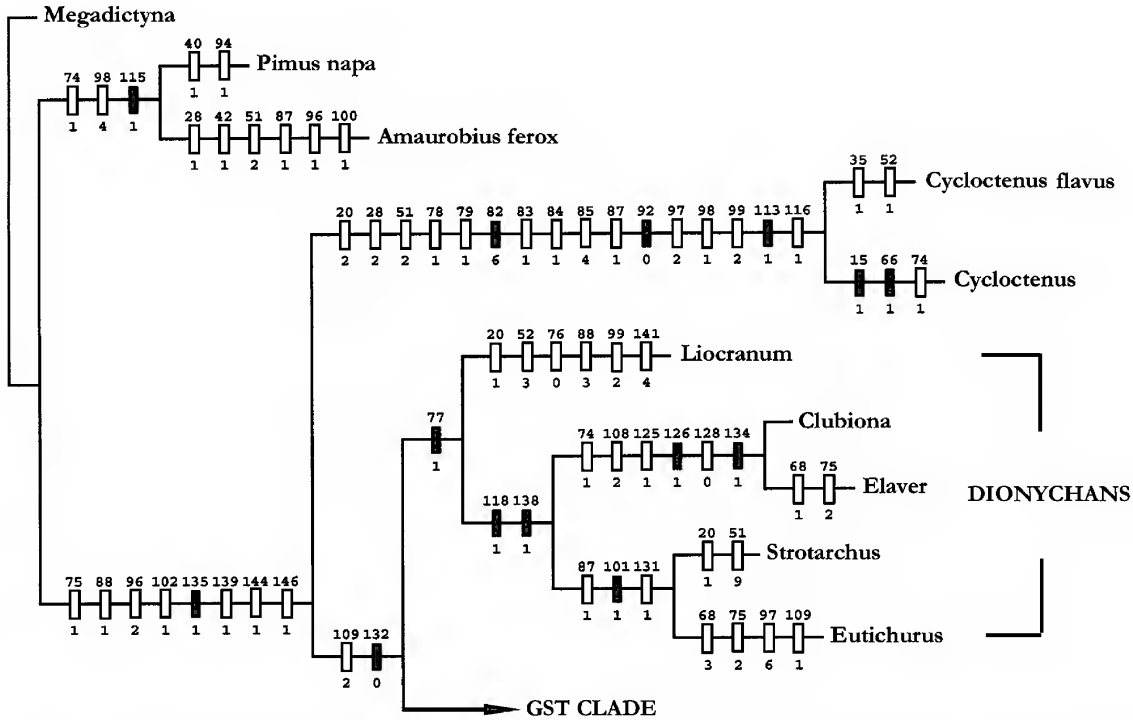

Fig. 3. Preferred cladogram (FIT = 1092.6, L = 813, CI = 32, RI = 67). Hashmarks = unambiguous character optimization, black = unique character transformation, white = homoplasious character.

lycosids, and pisaurids. This sister-group relationship is based on the occurrence of specialized parental care (char. 145), which originates in parallel in *Ancylometes*. The monophyly of the trechaleids + pisaurids clade (jak = 54%, BS = 1.5) is supported primarily by a tegulum broadly excavated and clearly exposing the subtegulum in ventral view (char. 29). Based primarily on the presence of a large, rather complex median apophysis (char. 46), *Neoctenus* is more closely related to *Trechalea* (jak = 86%, BS = 2.5) than to the zorids, where it is currently listed. The male tibial apex of *Neoctenus* does not show the typical membranous indentation as found in *Trechalea*; however, morphological and behavioral characters (personal obs.) suggest a closer affinity to *Paradossenus* F.O.P.-Cambridge, which appears to be a true trechaleid (Sierwald, 1993).

The monophyly (jak = 100%, BS = 8.4) of the two pisaurids, *Dolomedes* and *Thalassius*, is strongly supported by male genitalic characters; for example, the presence of a fulcrum (char. 30), embolic division with a basal membranous tube (char. 31), and a distal tegular process (char. 32). The monophyly of the lycosids (jak = 84%, BS = 2.3) is primarily based on their peculiar ocular pattern (char. 85) and an egg sac with a raised seam (char. 142).

Tengelloids (fig. 6) is an arbitrary name for designating an assemblage of tengellids, zorocratids, zoropsids, and phanoteans. This node is supported by the rather large subtegular/tegular interlocking lobes, which are clearly seen in unexpanded palps (chars. 27, 28), although they originate independently in some ctenids. Within this lineage, the tengellids are not monophyletic. *Titiotus*, *Liocranoides*, and *Anachemmis* cluster together at a node (jak = 68%, BS = 1.9) supported primarily by similarities in the male palp; for example, the bifid median apophysis (char. 49) and a lamelliform embolus (char. 51). By contrast, *Tengella* clusters with *Zorocrates* based on the oval shape of the ALE (char. 87) and the loss of a male tibial crack (char. 93). These two genera cluster with (*Uduba*

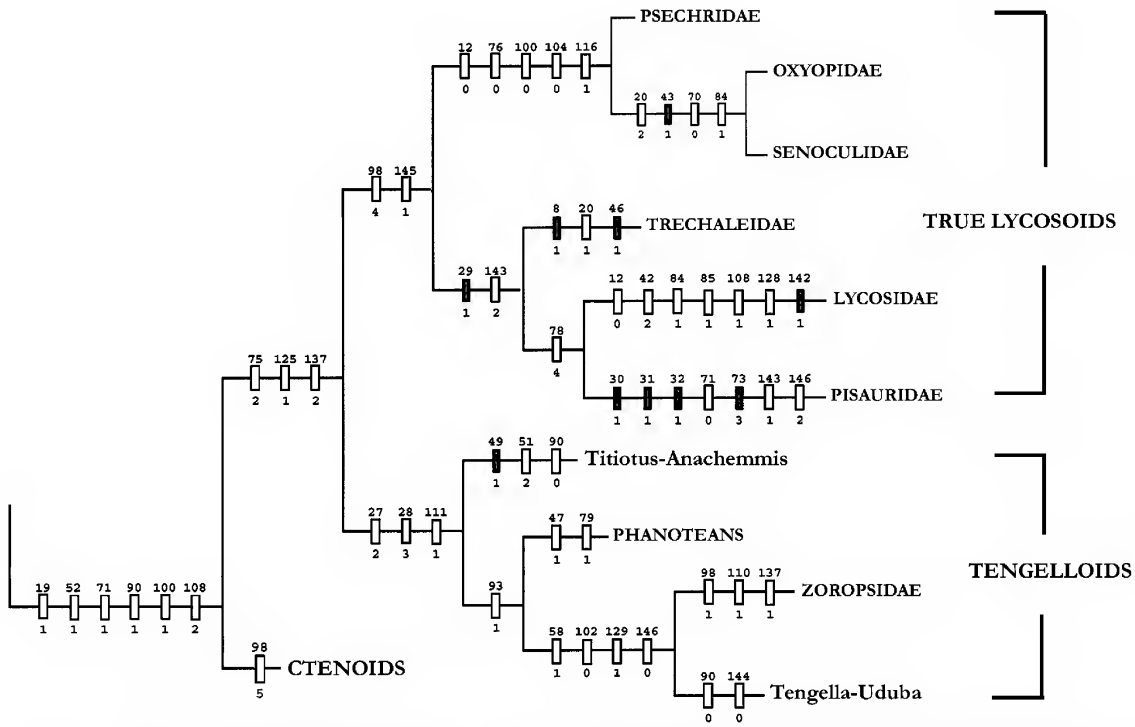

Fig. 4. Phylogenetic relationships for the grate-shaped tapetum (GST) clade as depicted in the preferred cladogram.

(*Raecius*, *Zorodictyna*)) based on a reversal to a canoe-shaped tapetum (char. 90) and an egg sac fixed to a web (char. 144), but their interrelationships are not yet well understood. However, the monophyly of the *Uduba* + *Zorodictyna* clade (jak = 90 %, BS = 2.4) is supported by the occurrence of a large, ventral tibial process on the male palpal tibia (char. 4), a carapace profile flattening posteriorly (char. 67), a reduction of the dorsal femoral spines (char. 96), and cribellate spigots distributed in small clusters (unknown in *Zorodictyna*). The monophyly of the *Phanotea* + *Griswoldia* clade (jak = 64%, BS = 1.1) is corroborated, and in this analysis it includes also a new genus from Chile. The strongest support for the phanoteans is provided by the cup-shaped median apophysis (char. 47), although it is independently derived in some ctenids. Although weakly supported, phanoteans appear to be sister to (*Zoropsis* (*Tengella* + *Zorocrates* (*Uduba*+ *Zorodictyna*))) based on the presence of a male tibial crack (char. 93), which is lost in the *Tengella* clade. The sister-group relationship (BS = 1.0) between zoropsids and *Tengella* + *Uduba* is supported by the epigynal lateral sectors with shallow atria (char. 58), which arise independently in *Anachemmis*; an oval calamistrum (char. 102), independently derived in the acanthoctenines; and a reversal to a divided cribellum (char. 129), although it is entire in *Raecius* + *Zorodictyna* and appears again in some acanthoctenines.

The evidence for the ctenoids (fig. 7) is still weak: the occurrence of a single pair of ventral spines near the apex of metatarsi I and II (char. 98). This lineage comprises at least three groups: the *Xenoctenus* + *Odo* clade, Miturgidae s.s, Zoridae s.s., and Ctenidae s.s. *Xenoctenus* and *Odo* branch off first as sister to the remaining ctenoids. A sister-group relationship between the Miturgidae s.s.+ Zoridae s.s. clade and the ctenids is based on a highly homoplasious character, that is, the occurrence of dense claw tufts (char. 106).

Neither miturgids nor zorids are shown to be monophyletic. *Neoctenus*, *Zoroides* Ber-

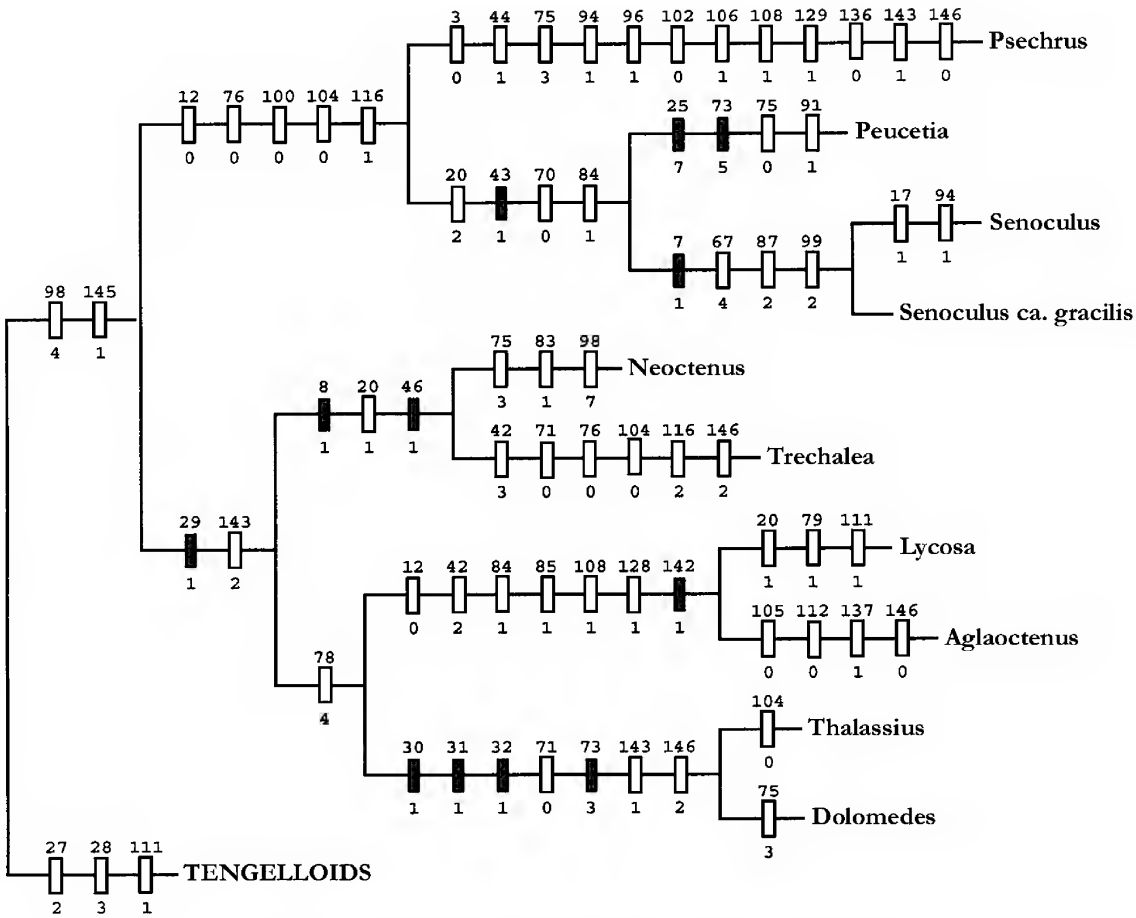

Fig. 5. Phylogenetic relationships for the lycosoid spiders.

land, *Odo*, and *Diallomus* are not closely related to Zoridae s.s. Although it was not included in the final matrix, previous analyses (Silva, unpubl.) showed *Zoroides* nesting with *Liocranum* based primarily on the laterally compressed posterior median spinnerets and the arrangement of the cylindrical spigots. The significance of these conditions is not yet clear but they may prove to be a synapomorphy of a more inclusive group within the dionychans, since they are also known among some gnaphosoids (Platnick, 1990: fig. 63). *Zoroides* lacks all the synapomorphies of the zorids and it has well-developed precoxal sclerites. These structures are unknown in any other zorid taxon, but in this study the occurrence of precoxal sclerites is unique to *Clubiona* and its relatives. Also, the ocular pattern of *Zoroides* does not resemble that in *Zora* or *Hestimodema*, but resembles instead that of *Liocranum*, which has a posterior ocular row almost straight. An ongoing taxonomic revision of *Zoroides* (Platnick, personal commun.) may help to elucidate the phylogenetic relationships of this taxon.

At the base of the ctenoid node (fig. 7) there is a clade (jak = 60%) comprising *Xenoctenus*, *Trujillina*, and *Odo*, but their interrelationships are not well determined. The support for this group is provided by the lobate shape of the epigynal lateral sectors (char. 53). *Odo* is shown to be polyphyletic. *Xenoctenus* clustered with *Odo* ca. *lycosoides* (jak = 76%). Although this sister-group relationship is based on homoplasious characters (chars. 71, 87), various genitalic characters, especially from the male palp, could

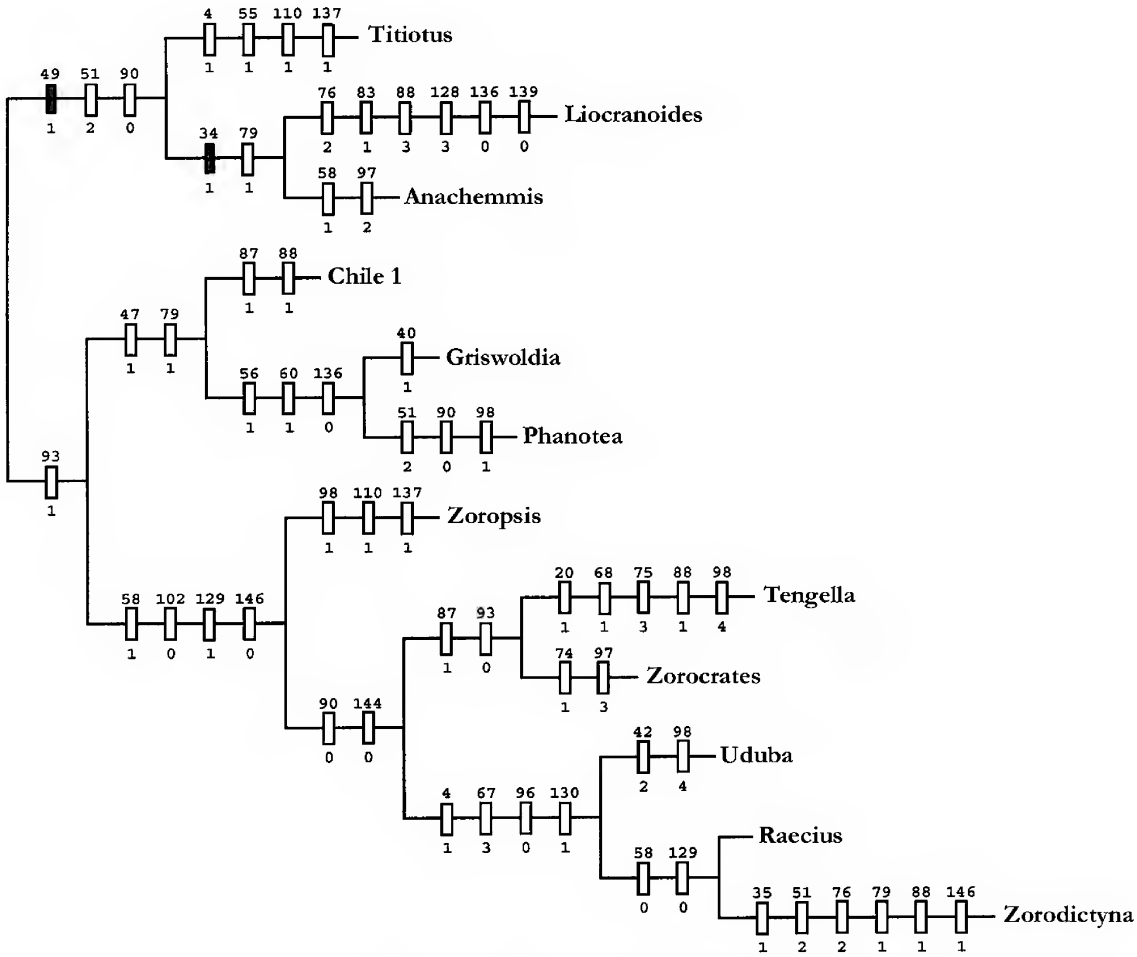

Fig. 6. Phylogenetic relationships for the tengelloid spiders.

corroborate the monophyly of this group in future studies. Conversely, *Odo* ca. *agilis*, presumably congeneric with the type species (Griswold, unpubl. notes), clusters with two other species (jak = 52%) based on male genitalic similarities (chars. 36, 38). Within the latter, a group of species close to *Odo obscurus* appears to belong to a new genus (personal obs.). On the other hand, *Trujillina* appears to be a monophyletic taxon (jak = 96 %, BS = 3.1), especially due to shared unique similarities of the male palp (chars. 14, 25, 51).

Zoridae s.s. (*Zora* + Australian taxa) comprises a monophyletic clade more closely related to Miturgidae s.s (*Miturga*, *Uliodon*, and *Teminius*). This sister-group relationship (jak = 64%, BS = 2.3) is primarily supported by male genitalic characters; for example, the presence of a retrolateral cymbial groove (char. 22), median apophysis opposite the embolic base (char. 45), and a coiled embolus arising near the middle of the tegulum (chars. 50, 51).

The monophyly of Miturgidae s.s. (fig. 8) (jak = 74%, BS = 1.5) is based on the posterior lateral spinneret distal segment being slender and as long or longer than the basal segment (char. 131), albeit this condition is convergent in *Eutichurus* and *Strotarchus*. An additional character supporting a close relationship among *Uliodon*, *Miturga*, and *Teminius* is the presence of long, strong macrosetae bordering the cymbial groove (char. 23), which is independently derived in some species of *Argoctenus*.

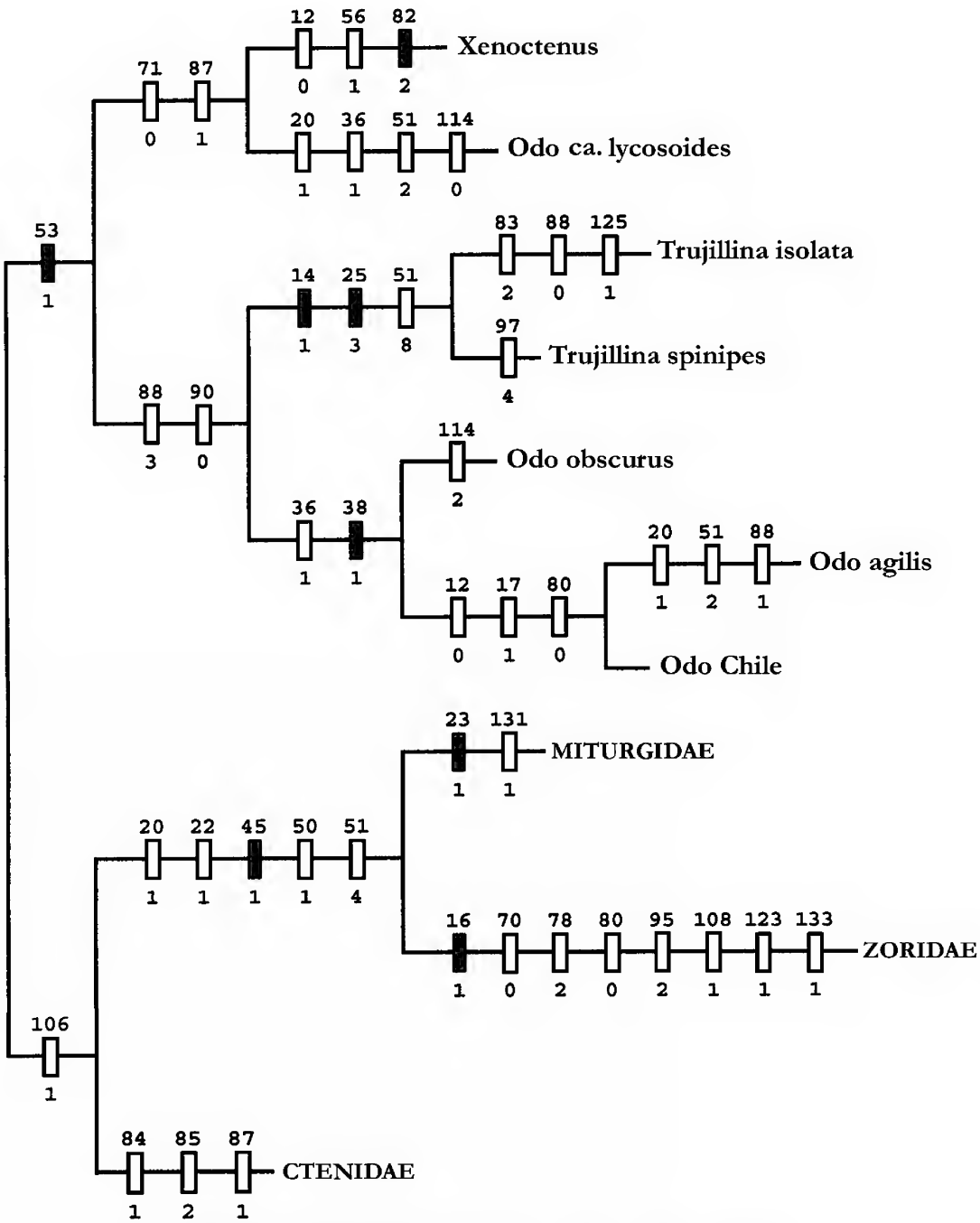

Fig. 7. Phylogenetic relationships for the ctenoid spiders.

The monophyly of *Zora* and Australian relatives (fig. 8) (jak = 100%, BS= 2.3) is supported by several somatic and genitalic characters, especially the male palpal configuration. Among the characters scored for this matrix are the occurrence of a characteristic process at the retrolateral tibial apophysis base (char. 16), median tracheae branching slightly (char. 123), and also a reduction in the number of piriform spigots

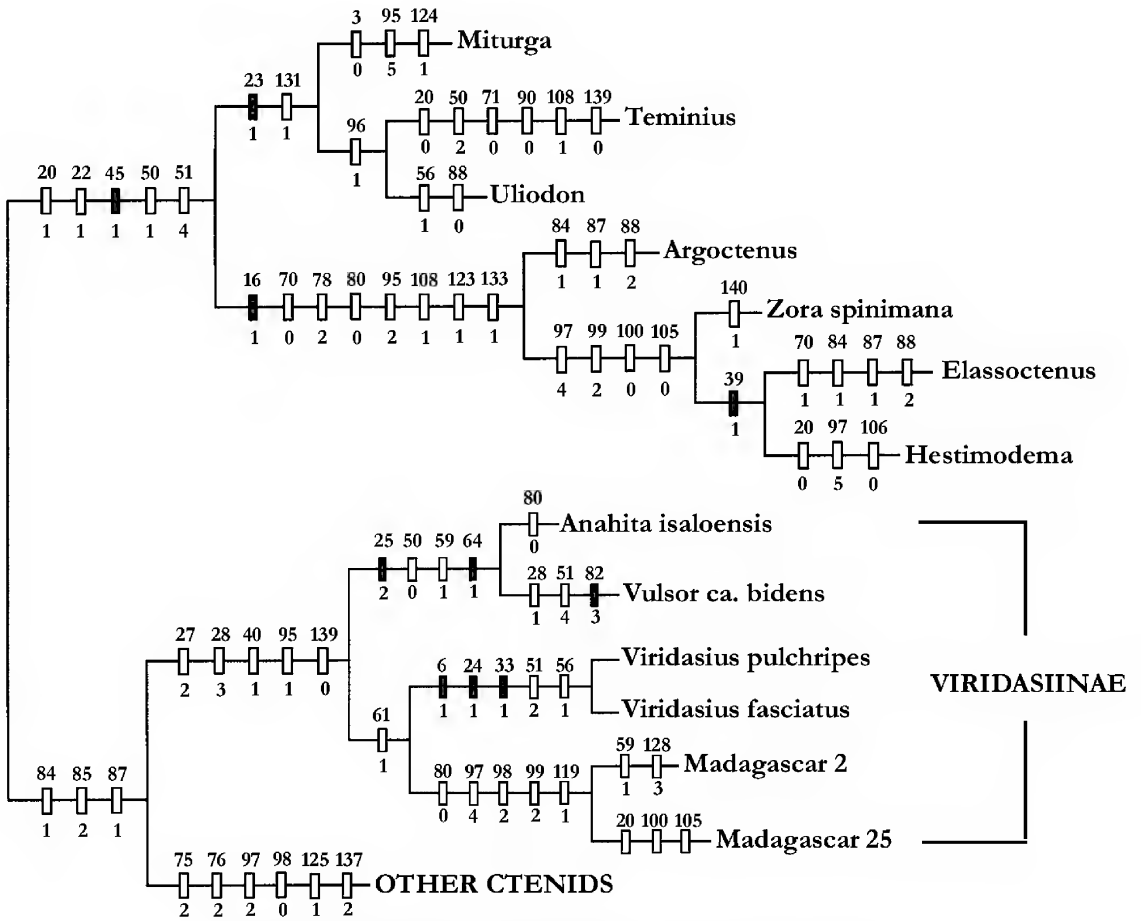

Fig. 8. Phylogenetic relationships for the ctenid spiders.

(char. 133). In general, the males of zorid spiders share a very characteristic hooked-shaped median apophysis, whereas the female internal genitalia exhibit also several characters in common, particularly the long, convoluted copulatory ducts. The interrelationships within zorids s.s. are not yet understood. Further studies are required to test the monophyly of the Australian zorid genera.

Ctenidae s.s. (fig. 8) (BS = 0.8) is primarily supported by a single unambiguous synapomorphy provided by their peculiar ocular arrangement (char. 85). Although a few other groups exhibit a 2–4–2 ocular pattern (e.g., the senoculids and the cycloctenids), the ctenidlike pattern, in congruence with other somatic and genitalic characters, helps to differentiate ctenids from other groups with three ocular rows (char. 84) and anterior lateral eyes oval in shape (char. 87). Despite lacking eyes, both *Janusia muiri* and an undescribed species from Australia nested within ctenids, stressing the importance of character congruence for delimiting monophyletic taxa.

Within the ctenids, at least five monophyletic groups were revealed, each corresponding in part to currently recognized subfamilies, of which only viridasines and acanthoctenines were shown to be monophyletic. Viridasines (fig. 8) (jak = 90%, BS = 1.2) comprise the most basal ctenid lineage. This group is primarily supported by a characteristic sclerotized tegular process at the conductor base (char. 40) and the presence of stiff setae on the ventral side of both male and female palpal tarsi (char. 95).

None of the characters supporting all other

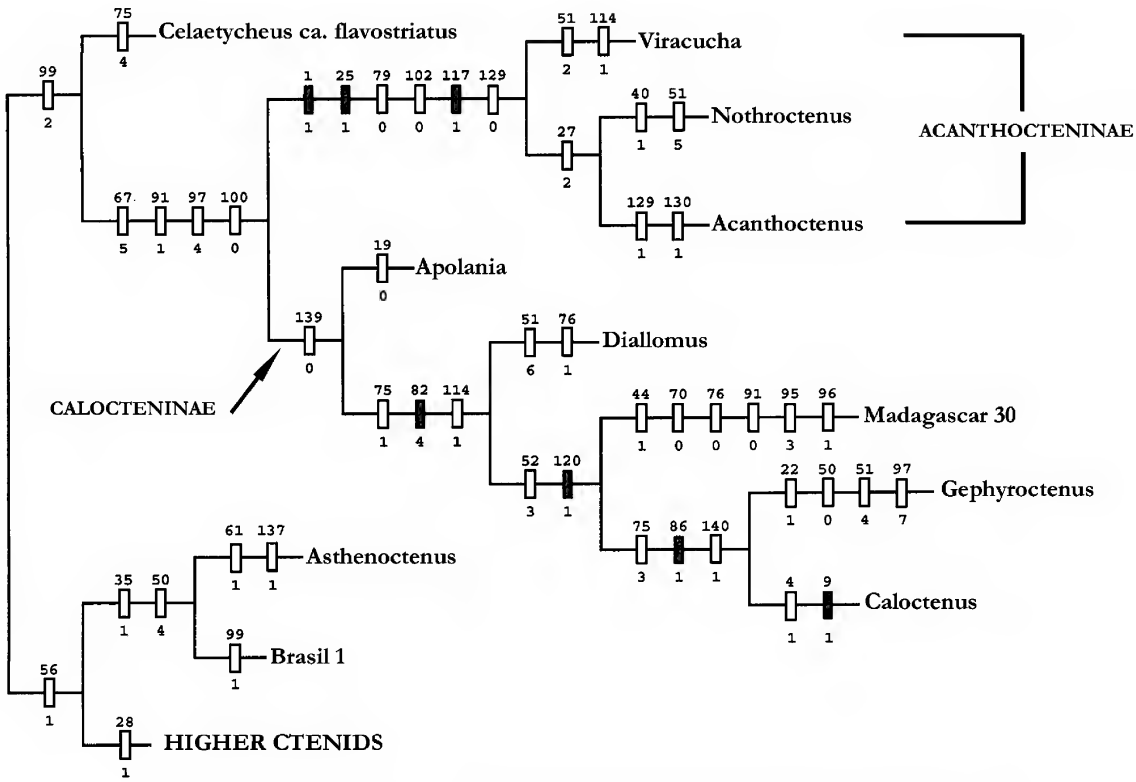

Fig. 9. Phylogenetic relationships for the acanthoctenine and caloctenine spiders.

ctenids is free of homoplasy. Among them are a short sternum (char. 76), at least five pairs of ventral spines beneath tibiae I and II (char. 97), at least three pairs of ventral spines beneath metatarsi I and II (char. 98), and the loss of epiandric spigots (char. 125). The most basal taxon at this node is not yet well determined (fig. 2) due to the uncertain relationships of a number of genera behaving as "wildcard" taxa throughout the study: *Asthenoctenus*, *Cupiennius*, *Ancylometes*, *Janusia*, and *Celaetycheus*.

In the working hypothesis (fig. 9), *Celaetycheus* clustered with the acanthoctenines and caloctenines. The evidence for this relationship is provided by a highly homoplasious character, that is, the occurrence of strongly overlapping tibial spines (char. 99). In turn, the sister-group relationship between acanthoctenines and caloctenines is supported by a carapace slightly to strongly indented at the thoracic fovea (char. 67); an opaque grate-shaped tapetum (char. 91), albeit this condition is reversed in *Acanthoctenus* and in some caloctenines; more than six pairs of ventral paired spines beneath tibiae I and II (char. 97), independently derived in some other groups; and secondary loss of the most distal pair of ventral spines beneath tibiae I and II (char. 100).

Acanthocteninae (fig. 9) is shown to be monophyletic (jak =100%, BS = 5.9) based on a globose palpal patella (char. 1), a large retrobasal cymbial process (char. 25), a reversal to an oval calamistrum (char. 102), and a tarsus with a dorso-distal V-shaped indentation (char. 117).

Caloctenines (jak= 68%) as currently delimited are shown to be polyphyletic. *Anahita* and *Trujillina* belong elsewhere. Also, this analysis indicates that *Diallomus* is a caloctenine and not a zorid. Calocteninae (fig. 9) is primarily supported by the occurrence of thickened, elongated anal setae (char. 127), although this is an ambiguous optimization (it is still unknown in *Apolania*). Caloctenines are also characterized by a reduced number of cylindrical gland spigots (char.

139), although this condition occurs independently at some other nodes.

Within the caloctenines, *Apolania* is sister to all other taxa, but its position is not yet well determined. In turn, *Diallomus* is sister to a clade comprising a new genus from Madagascar, *Caloctenus*, and to *Gephyroctenus*. The monophyly of the latter group (jak = 56%) is supported by the small, distally rounded labium (char. 82), among other homoplasious characters. The sister-group relationship between a new Malagasy genus and the other two caloctenines (jak = 70%) is primarily based on the occurrence of leaf-shaped setae (char. 120). The sister-group relationship between *Gephyroctenus* and *Caloctenus* (jak = 68%) is supported by a great reduction of the anterior lateral eyes lenses (char. 86).

The other main ctenid lineage comprises the so-called higher ctenids (figs. 9, 10). This group is based on the presence of epigynal lateral processes (char. 56), although they originate independently elsewhere. Within this clade there are at least four subgroups; however, their relationships are not yet well determined. The working hypothesis shows *Asthenoctenus* and an undescribed genus from Brasil at the base of this group; the latter resembles *Enoploctenus* in the almost flattened and broad carapace as well as in the presence of hair pencils, although they are not as dense. Although this new taxon has a male and female genitalic structure rather unusual for most ctenids, further studies might prove that indeed it belongs in the Acantheinae.

Within the higher ctenids (fig. 10), *Janusia*, *Leptoctenus*, and *Anahita* were joined at a node (jak = 62) based on the copulatory openings marked by transparent alveoli (char. 54) and on lateral sectors with posterior fingerlike processes (char. 57). The monophyly of the *Leptoctenus* + *Anahita* clade (jak = 52%) is primarily based on a loss of the retrolateral tibial apophysis (char. 12) and on the presence of a retrolateral tibial spine (char. 17). Neither *Leptoctenus* nor *Anahita* is monophyletic. Whereas a new Australian species of *Leptoctenus*, close to the type species (Raven, personal commun.), is sister to *Anahita*, *L. byrrhus* belongs in the ctenine clade (fig. 11) where it is presumably most closely related to a group of Southeast Asian species.

On the other hand, *Anahita isaloensis* Ono clustered with a new species of *Vulsor* close to the type species (examined). Based on these results and the examination of several other somatic and genitalic characters, the former species is removed from *Anahita* and transferred to *Vulsor*.

In the working hypothesis (fig. 10), *Cupiennius* and *Ancylometes* clustered together based on characters primarily provided by the leg spination pattern (chars. 97, 98) as well as a reversal to three tarsal claws (char. 110), none of which is free from homoplasy. These two genera are placed at the base of a group in turn also supported by highly homoplasious characters; for example, by the occurrence of four cheliceral teeth on the retromargin (char. 75). Although the interrelationships within this latter group are far from being elucidated, it appears that it consists of at least two major lineages, corresponding to the ctenines and the acantheines.

The main support for the ctenine + acantheine node is the modification of the epigynal median sector into a smooth plate (char. 55), albeit independently derived in *Titiotus*. Although the occurrence of a cup-shaped median apophysis (char. 47) appears to define a monophyletic lineage, more exhaustive studies are needed to determine the interrelationships within this subgroup. A secondary loss of the bimarginate median apophysis (char. 48) further supports a sister-group relationship between ctenines and acantheines (fig. 11).

In turn, within this last group of ctenine spiders there appears to be at least one monophyletic lineage comprising *Thoriosa* and a new genus from Australia and Asia. This sister-group relationship is primarily based on synapomorphies provided by both male and female genitalia. Additionally, further studies might prove the monophyly of a second group supported by the presence of an apical lamella on the retrolateral tibial apophysis (char. 13). However, the composition of this clade is still rather vague (a new species from Tanzania lacks a retrolateral tibial apophysis, whereas *Leptoctenus byrrhus* is still scored "?" for this character because of uncertainties in homologizing its condition).

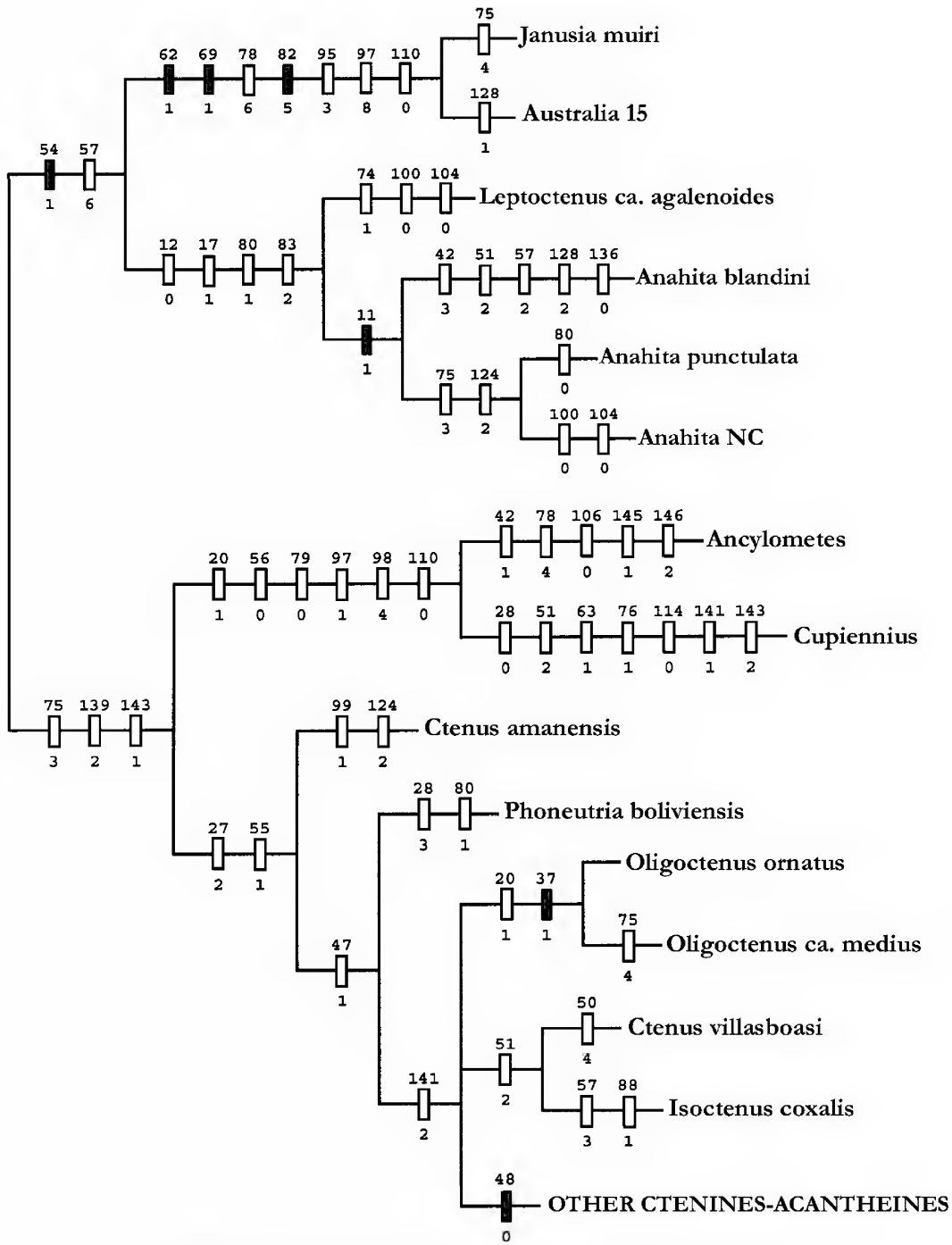

Fig. 10. Phylogenetic relationships for the "higher ctenids".

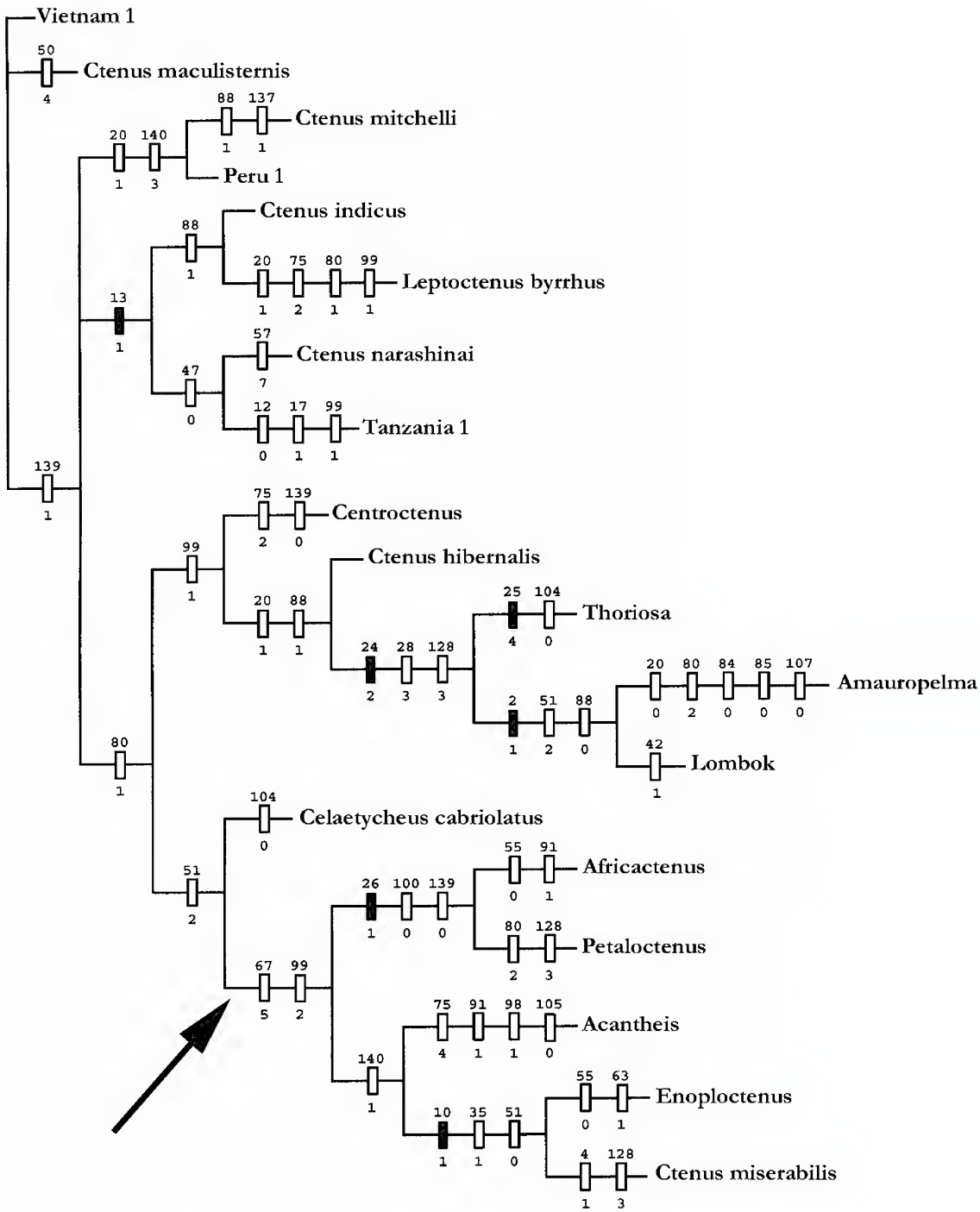

Fig. 11. Phylogenetic relationships for the acantheine spiders.

Despite their rather low support (chars. 67, 99, which originate in parallel at least three times), acantheines (fig. 11) appear to comprise a monophyletic group. Within this clade, a sister-group relationship between *Africactenus* and *Petaloctenus* is supported by unique similarities in the male genitalia (e.g., a cymbial ventral process; char. 26). Although still weakly supported, it appears that *Acantheis* is sister to a clade comprising *Enoploctenus*. In turn, the latter is most closely related to a clade comprising *Ctenus miserabilis* Strand; this relationship is primarily based on the structure of the male palp (e.g., the deeply notched and setose palpal tibia; char. 10).

DISCUSSION

The results of this study are consistent with the hypothesis of a polyphyletic Ctenidae as this family is currently delimited. However, the present data support a monophyletic group excluding just *Trujillina* and *Itatiaya*—eight monotypic genera were not included in this analysis, and current work shows they belong elsewhere. Although the type species of *Itatiaya* was not examined, the original description (Mello-Leitão, 1915) suggests it is a member of the *Odo* clade, and ongoing revisionary work of the Neotropical zorids will clarify the taxonomic status of this peculiar clade (Baptista, personal commun.). Also, my study shows that *Janusia*, *Ancylometes*, and *Diallomus* are indeed members of the Ctenidae s.s.

Ctenoid Relationships

At this level of analysis the presence of a cribellum does not help to define unambiguously any major clade. However, the loss of the calamistrum is still an unambiguous synapomorphy shared by all examined families except the amaurobiids.

This cladistic analysis still supports a major group based on the grate-shaped tapetum in the posterior median eyes. However, accepting this more inclusive clade (GST) as the Lycosoidea implies several reversals and losses in various characters, including the grate-shaped tapetum itself. This character has reversed at least three times to the canoe condition in such taxa as the tengellids, zorocratids, *Trujillina*, and *Odo*. Further, the tapetum appears to be secondarily lost in most species of true zorids (personal obs.).

Within the GST group, the oval calamistrum, which was regarded as an unambiguous synapomorphy for tengellids, zorocratids, and lycosoids (Griswold et al., 1999: 59), provides ambiguous support for a rather similar group. Some of the clades retaining an oval calamistrum are the psechrids among the true lycosoids, zoropsids and zorocratids among the tengelloids, and the acanthoctenines among the ctenoids.

These results corroborate the monophyly of the higher lycosoids (Griswold, 1993), and based on them I suggest that Lycosoidea should be restricted to the psechrids + lycosids clade. This new group comprises six monophyletic families: Lycosidae, Pisauridae, Trechaleidae, Psechridae, Senoculidae, and Oxyopidae.

The other two major clades within the GST group (i.e., tengelloids and ctenoids) are still weakly supported. In fact, their relationships are based on highly homoplasious characters, and therefore their positions might change in future studies. However, within the tengelloids there are at least three well-defined subgroups—*Titiotus* + *Anachemmis*, *Phanotea* + *Griswoldia*, and *Uduba* + *Raecius*—all of which cluster at a node supported by the tegular/subtegular interlocking lobes, which are shared with some ctenids. The *Phanotea* and *Uduba* clades share the suture on the male tibiae, a condition also found in *Zoropsis*. Unfortunately, I was not able to demonstrate the monophyly of a more inclusive group supported by the tibial crack, which appears to be independently derived two or three times, depending on the final placement of the phanoteans, a taxon formerly thought to belong in the ctenoids (Griswold, 1993). The final position of the phanoteans is decisive because they include the genus *Griswoldia*, which is currently the putative sister group to Ctenidae (Griswold, 1993).

Among the tengelloids, *Zoropsis* shares many more characters, albeit homoplasious, with the phanoteans than with any of the remaining taxa; however, in this analysis, the occurrence of a cribellum apparently overrules the support from less homoplasious characters. Further analyses involving a more

detailed examination of relevant taxa and additional characters may prove that both tengellids and zorocratids belong elsewhere, whereas *Zoropsis* may indeed be sister to the phanoteans.

None of the analyses conducted corroborated a sister-group relationship between *Zoropsis* and *Acanthoctenus*, as has previously been argued (Griswold, 1993). However, such a group was found after the inclusion of two dummy synapomorphies. The addition of a single dummy character did not affect relationships at all. This test showed *Zoropsis* and the acanthoctenines clustering together and in turn forming a sister-group relationship with *Zorocrates*. However, an alternative hypothesis showed *Zoropsis* + *Acanthoctenus* sister to a clade comprising the tengelloids, lycosoids, and ctenoids. Also, these new topologies support a single unambiguous origin for the cribellum, but psechrids were moved to a more basal position, right after amaurobiids. Psechrids were placed as sister to a clade comprising (udubiids (*Tengella* (*Zorocrates* + *Zoropsis*))). Additionally, these topologies showed the (oxyopids + senoculids (cycloctenids)) clade within Ctenidae as sister to the caloctenines. This relationship was based on characters provided by the spination pattern and the claw tufts. Interestingly, this new arrangement did not increase the number of steps (L = 813, CI = 33, RI = 67); however, the two synapomorphies solely shared by *Zoropsis* and the acanthoctenines have not been found yet.

As mentioned above, *Trujillina* appear to be most closely related to *Odo* s.s., and both together are sister to a clade comprising *Xenoctenus* and *Odo* ca. *lycosoides*. Interestingly, this entire clade does not fit in any of the currently known ctenoid families. Members of the *Xenoctenus* clade have epiandrous spigots, which, in addition to the oval-shaped anterior lateral eyes, the posterior median eyes grate-shaped tapetum, and dense metatarsal and tarsal scopulae (though they lack claw tufts), makes them resemble some of the most basal ctenids belonging to viridasines, in particular *Vulsor*. A revision of the South American zorids (Baptista, in prep.) should provide more evidence for elucidating the phylogenetic placement of this lineage, members of which resemble some miturgids and viridasines also in some other primitive characters; for example, a reduced spination pattern beneath metatarsi I and II, as well as the prolateral tibial spines on the male palp (two distals plus one apical).

Although the preferred hypothesis supports the true miturgids + true zorids clade as the sister group of the Ctenidae, based on characters shared with the viridasines, forcing a sister-group relationship between phanoteans and ctenids (replacing char. 15 with a dummy synapomorphy) increased the length of the most parsimonious trees by only a single step (L = 814, CI = 32, RI = 67). In fact, less homoplasious characters were better optimized on this tree. Unfortunately, a synapomorphy uniting *Phanotea* + *Griswoldia* with the ctenids has not yet been found. So far, the characters shared by those taxa, especially those from the male genitalia, occur only among some of the ctenines, which exhibit the widest range of genitalic variation among ctenids and thus are still very hard to characterize as a group.

Ctenid Phylogeny

The monophyly of ctenids is supported by the typical ocular arrangement (fig. 27b). Despite the presence of a similar condition in some cycloctenids, members of that group have several unique characters that help to separate them from the ctenids at first glance (e.g., a male palp with several, large cymbial spines, and the modified bent tarsi with three large claws). Also, based primarily on similarities in the structure of the tapetum and the laterigrade condition, it has been proposed that cycloctenids are a subfamily of the Selenopidae (Homann, 1968, 1971: 236). However, further studies, including a thorough sampling of dionychans (Coddington and Levi, 1991), are needed in order to better establish the position of this group.

Although the relationships among ctenids are not yet well determined, it appears that this family comprises at least eight lineages, five of which correspond in part to known subfamilies: the viridasines, acanthoctenines, acantheines, caloctenines, and ctenines. Of these, the viridasines are shown to be the most basal clade of the family. Other cladis-

tic analyses (Silva, 2001) agree also in the monophyly of these lineages based on genitalic characters; however, they appear weakly supported with the present data. Because of the great variation observed in both male and female genitalia across the examined taxa, it was not possible to include more genitalic data without an increase in the number of terminals, which would be irrelevant to the objectives of this study.

On the other hand, all the most parsimonious trees show *Ancylometes* clustering within Ctenidae, and although its position is still not well understood, it appears to be sister to *Cupiennius* and that together they form a group that might be basal to the higher ctenids. The support for this relationship is rather low (i.e., primarily the occurrence of four ventral paired spines beneath tibiae I and II, and a reversal to three tarsal claws); however, it is the best explanation at hand. Attempts to force the inclusion of *Ancylometes* within Pisauridae failed at all times despite being compared to the most similar taxa in both morphology and behavior (i.e., *Dolomedes* and *Thalassius*). Therefore, their similarities have to be explained as independently derived, at least twice, presumably as an adaptation to similar living conditions (such as streams and swamps).

Celaetycheus is shown to be polyphyletic. The Central American species belong elsewhere within the ctenines, whereas a new species, congeneric with the type specimen, is sister to the acanthoctenines and caloctenines; however, the position of *Celaetycheus* s.s. is not yet well understood. A taxonomic revision of this genus is under way (Brescovit, personal commun.) and may help to elucidate the relationships of these small spiders (about 4 mm body length).

Another genus of uncertain position is *Asthenoctenus*. This taxon appears basal to a clade comprising *Janusia*, the ctenines, and the acantheines, but it may have a more basal position, as suggested by similarities with some viridasines in the female internal genitalia, which, interestingly, are shared also with *Phanotea*.

Although these results suggest that *Janusia* is sister to the *Anahita* + *Leptoctenus* clade based on genitalic similarities, problematic for resolving the placement of this genus is the still unknown male of *Janusia muiri*, the type species, which is known from a single adult female and a few juveniles; briefly, this is a terminal represented in the matrix by about 54% unknown entries, and therefore its position must be regarded as uncertain.

Although *Apolania* appears to be sister to all other caloctenines, these results are also tentative. This terminal shows 32% unknown entries because it is represented by a single male specimen, the only one known in world collections (in addition to one male palp representing the holotype). Additionally, its small size, roughly 4 mm, made it very hard to examine somatic characters without damaging the specimen; hence, the position of this genus might easily change with further studies.

On the other hand, my analysis shows that *Diallomus* belongs in the caloctenines. Furthermore, this analysis clearly shows that *Elassoctenus* belongs to a monophyletic group comprised by *Zora* and close relatives. From all of the above, the synonymy of *Diallomus* with *Elassoctenus* is unfounded (contra Lehtinen, 1967: 228), and based on the examination of the type specimens of both genera as well as some other new species, I consider *Diallomus* to be a valid genus of Ctenidae.

Homoplasy and Character Support

The high levels of homoplasy, either by repeated convergences or reversals, which are often observed in large datasets have already been pointed out in the spider literature (Griswold et al., 1999: 61; Coddington and Levi, 1991). Despite their apparent lack of phylogenetic signal, however, some homoplasious characters appear to play a key role in defining higher-level taxa (i.e, when one of these noisy characters is deactivated, the resolution of a particular group may be lost).

Among spiders the leg spination pattern tends to have a great deal of variation at the family level. This variation is clearly exemplified by the ctenids. In this group, tibial spines are often stable within genera, whereas metatarsal spines tend to be species-specific; however, the range of variation within this family extends from 3 to more than 10

pairs of spines beneath tibiae and metatarsi I and II. The tibial spination has a length of 21, CI of 9, and RI of 56, whereas the metatarsal spination has a length of 27, CI of 25, and RI of 54. Despite their great variation, both characters provide additional support for a clade comprising the so called higher ctenids which are characterized by having five tibial pairs and only three metatarsal pairs of spines on legs I and II.

Ctenids have been described as two-clawed spiders, and this is one reason for questioning the taxonomic position of both *Cupiennius* and *Ancylometes*, which have a relatively small inferior tarsal claw (ITC). However, a large ITC is present in both males and females of a new species of *Caloctenus* from Peru as well as in an undetermined species from Ecuador. Interestingly, the occurrence of an ITC in the first and second instar of some ctenids (Homann, 1971: 264) was verified by examining early instars of *Oligoctenus medius*, *Cupiennius salei*, and *Phoneutria keyserlingi*; the former showed a reduced ITC, markedly contrasting with a more typical claw observed in *Cupiennius* (this genus has a much reduced ITC in the adults). It appears that the ITC is lost very early in the development of many ctenid spiders; the examination of nymphs of *Phoneutria* with eyes already developed showed no traces of an ITC. Although ontogenetic comparisons are beyond the scope of this study, such an approach might corroborate the occurrence of an ITC as an ancestral condition for the ctenoid spiders and thus help to better determine the position of basal taxa within this group.

The epiandrous spigots (L = 5, CI = 20, RI = 82) appeared very promising at the onset of this study, but they proved to be very difficult to homologize. Although a more general pattern could be represented by isolated dispersed spigots, this is still hard to code for a phylogenetic analysis because those spigots may be scattered along the epigastrium (López and Emerit, 1988: fig. 5) either in a continuous straight line along the edge (López and Emerit, 1988: fig. 8) or in a line broken near the middle, as in *Pimus napa*. The variation of spigots may also involve the occurrence of both isolated and clustered spigots; for example, several spigots arising from the same socket, more or less distributed on a broad surface of the epigastrium, as in *Uliodon tarantulinus* and one species of *Vulsor*, or along a narrow transverse line, as in *Miturga lineata*. A more common arrangement in the examined taxa is the occurrence of two groups of spigots, either isolated, as in *Amaurobius ferox*, or in clusters, as in some zorids as well as some *Vulsor* and Madagascar 2 (new genus; Silva, 2001) species. Another arrangement involving several clusters along a transverse line was observed in *Odo* ca. *lycosoides* and one species of *Viridasius*. The examination of the male epigastrium showed also the occurrence of pores, which may correspond to the gonoporal organs, apparently present in practically all male spiders (López, 1974; López and Emerit, 1988), but in this study they were observed only in some of the specimens examined.

In this analysis, *Zorocrates* clustered with *Tengella*. One of the characters supporting this relationship is the loss of the tibial crack, which appears to originate at least twice. Interestingly, this suture is present in a number of Australian species still of undetermined status, many of which also show a tarsal rod as in *Griswoldia acaenata* (Griswold, 1994). Among these Australian taxa, there is a new genus (Raven, personal commun.), that has male and female genitalia resembling those in *Zorocrates*; however, this taxon has a well-developed suture on all the legs. To what degree the tibial crack is a product of convergence or a synapomorphy for a more inclusive group uniting phanoteans, zoropsids, and zorocratids still awaits resolution.

Taxonomic Implications

Based on this study, *Tunabo* Chamberlin, 1916, is synonymized with *Neoctenus* Simon, 1897, and the latter is transferred from the Zoridae to the Trechaleidae. The type species, *Tunabo peruvianus* Chamberlin, 1916, is based on an immature male that was seemingly ready for its last molt. The holotype (MCZ 322) exhibits the typical habitus of *Neoctenus* (i.e., carapace and abdomen yellowish with two grayish lateral bands, and a brush of long, silky hairs projecting from the ocular region as is also observed in *Cen-*

troctenus and *Anahita*); most importantly, however, it has already developed a median apophysis almost similar to that found in *Neoctenus* (fig. 16d). On the other hand, *Neoctenus comosus* Simon, the type species (female holotype, MNHN 7223) and at least two new species from Peru and Colombia exhibit the typical lycosid eye pattern (fig. 25d); however, the male and female genitalia closely resemble those found in trechaleids, in particular those of *Paradossenus* (see Brescovit et al., 2000: figs. 1, 2).

This study also indicates that *Xenoctenus* Mello-Leitão is not a synonym of *Tunabo*, and it is here considered a valid genus, although its affinities are not yet clear. The cladistic analysis suggests it is sister group of a new species of *Odo*, in turn more closely related to *Odo lycosoides* (Chamberlin) (female holotype, MCZ 254). This relationship is supported by various synapomorphies provided by both male and female genitalia (all unique to the *Odo* clade); however, only a few were included in this study since members of this group (currently listed as neotropical zorids) are being subjected to an in-depth taxonomic revision (Baptista, personal commun.). Strong evidence for a sister-group relationship between *Xenoctenus* and a group of species closely related to *Odo lycosoides* is also provided by the tapetum: within the *Odo* clade, only some species exhibit a well-developed, shiny, grate-shaped tapetum (personal obs.), for example, those most closely related to *X. marmoratus* and *O. lycosoides*.

This study also indicates that *Ancylometes* Bertkau does not belong in Pisauridae and, primarily supported by the ctenid eye pattern and similarities of both male and female genitalic structure, this genus is transferred to the Ctenidae. Although the phylogenetic relationships of this genus are also not clearly determined, it appears that it may belong to a basal group of ctenids where a median tarsal claw is still retained.

Even though *Elassoctenus* Simon, 1909 is considered a senior synonym of *Diallomus* Simon, my results indicate that the former is a valid genus of the Zoridae, whereas *Diallomus* is actually a member of the Ctenidae. The type species of *Elassoctenus*, *E. harpax* Simon (male holotype, MNHN 24343), has a male palpal structure resembling that found in *Zora* and Australian relatives (e.g., *Hestimodema*, fig. 17a). On the other hand, the type species of *Diallomus*, *D. fuliginosus* Simon (female holotype, MNHN 16.259), shares with *D. speciosus* Simon a sausagelike spermathecae and a rather short spermathecal chamber and, in turn, *D. speciosus* shares with other new species assigned to this genus a very unique male palpal structure. Also, the cladistic analysis suggests that *Diallomus* is a member of the caloctenines and that this relationship is primarily supported by the occurrence of long, thick anal setae and a flattening of the anterior lateral eyes lenses (e.g., fig. 25h).

Finally, the examination of additional material (including some from the type locality) shows that *Anahita isaloensis* Ono, 1993 comprises two different species and that both actually belong in *Vulsor* Simon. It also appears that both species belong to a group most closely related to *V. bidens* Simon, the type species. Several new specimens share with the holotype (NSMT-Ar 3023, not examined, Ono, 1993: fig. 2) a similar male palp. On the other hand, the second specimen (NSMT-Ar 3024, not examined, Ono, 1993: fig. 4) has a male palp similar to some other specimens which have been assigned to a new species (Silva, 2001).

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APPENDIX 1

Character Descriptions

MALE PALP

1. Palpal patella: normal (0); swollen (1).
Weight = 10, L = 1, CI = 100, RI = 100
Most examined taxa have an unmodified, roughly convex patella. State 1 refers to the swollen patella observed in the acanthoctenines (e.g., *Viracucha andicola* Lehtinen, 1967: fig. 416).

2. Retrolateral patellar processes: absent (0); present (1).
Weight = 10, L = 1, CI = 100, RI = 100
Changes in the shape of the patella may also involve either presence of small retrolateral thornlike processes or a retrolateral projection directed outwards (e.g., the patellar process found in *Liocranoides*; Platnick, 1999: fig. 11). All these retrolateral patellar processes appear to be independently derived. Within the ctenid spiders, their presence is an apomorphy of a new Australasian genus, *Amauropelma* Raven et al., 2001, represented in this study by two species, one from Indonesia (Lombok, CDC) and a second from Australia (Australia 1, QLM). However, a few species of *Amauropelma*, either from Australia or Southeast Asia, lack any kind of patellar modifications (Raven et al., 2001; Silva, 2001).

3. Dorsal tibial processes: present (0); absent (1).
Weight = 6.0, L = 5 (4 extra steps), CI = 20, RI = 0
Although a restricted distribution of dorsal tibial processes in various spider families suggests that these changes are a derived condition wherever they occur (Griswold, 1990: 16), they tend to be more common in basal groups, for example, the nicodamids (Harvey, 1995: 283; Forster, 1970: fig. 109) and amaurobiids (fig. 12). Dorsal processes were scored for *Megadictyna*, *Amaurobius ferox*, *Miturga lineata*, *Psechrus*, and *Cycloctenus flavus* (Hickman, 1981: fig. 8).

4. Ventral tibial processes (char. 3, Griswold, 1993): absent (0); present (1).
Weight = 6.0, L = 5 (4 extra steps), CI = 20, RI = 42
Ventral processes have arisen independently in various spider groups (Griswold, 1990: 15). Several taxa examined in this study exhibit a range of apical or subdistal processes, in addition to the RTA. Only those taxa having a well-defined lobate process were scored for state 1. These processes (e.g., Griswold, 1993: figs. 20, 26) are independently derived in the (*Raecius*, *Uduba*, *Zorodictyna*) clade, as well as in *Titiotus* (fig. 13c), *Tengella*, *Janusia* n.sp., *Caloctenus*, *Africactenus*, and *Apolania*.

5. Basal tibial apophyses: absent (0); present (1).
Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 50
In addition to the RTA, both species of *Trujillina* have developed large, retrolateral, and bifid apophyses at the base of the tibia (fig. 14). Similar apophyses are lacking in other examined taxa.

6. Retrobasal tibial processes: absent (0); present (1).

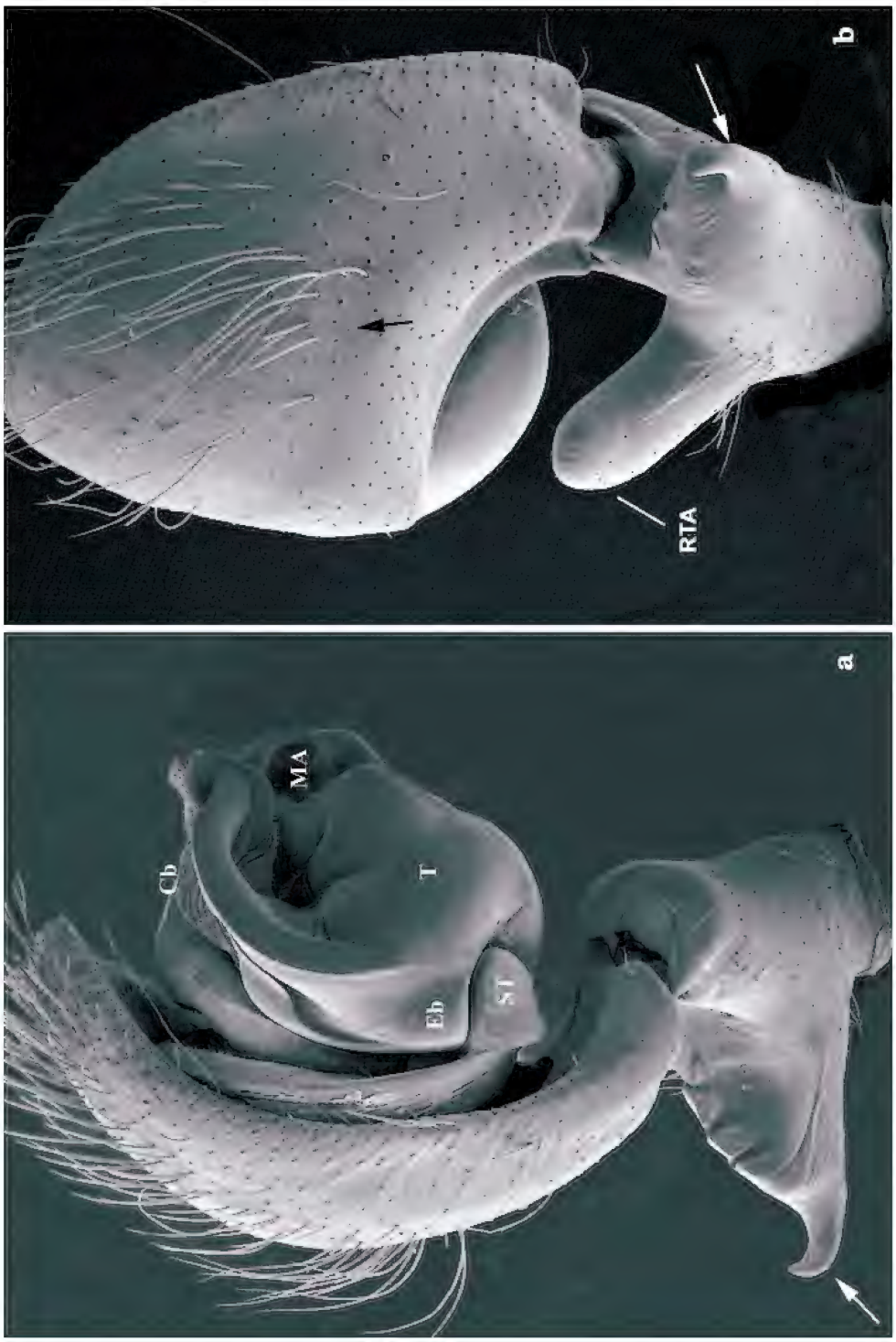

Fig. 12. *Amaurobius ferox* (Walckenaer). **a.** Left male pap, prolateral view. **b.** Same, dorsal view, black arrow points to trichobotrium. White arrows point to dorsal tibial apophysis. Cb = conductor base, Eb = embolic base, MA = median apophysis, ST = subtegulum, T = tegulum.

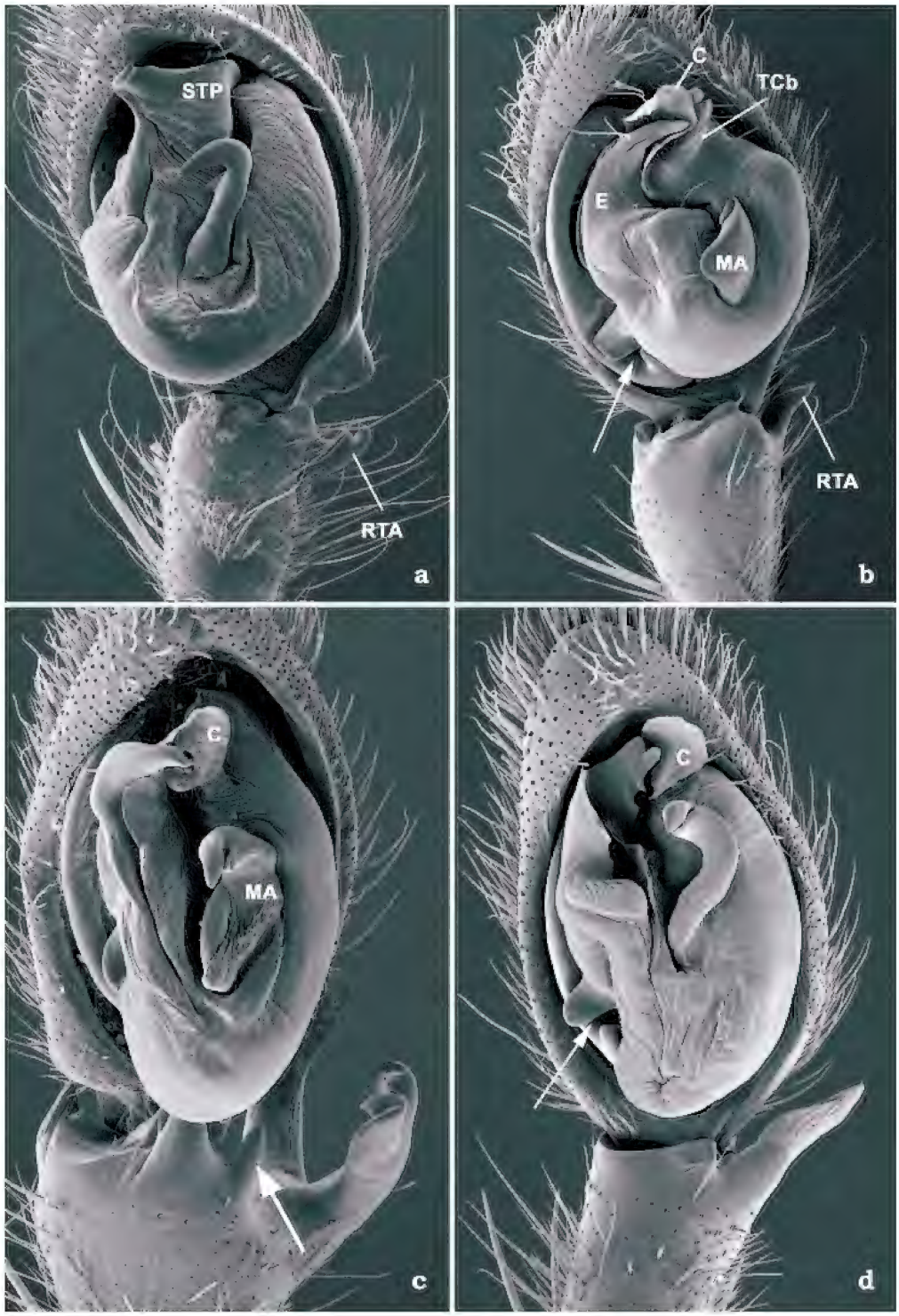

Fig. 13. Left male palp, ventral view. **a.** *Zorocrates* cf. *guerrerensis* Gertsch and Davis. **b.** *Griswoldia acaenata* (Griswold). Arrow points to subtegular/tegular interlocking lobes. **c.** *Titiotus* sp. Arrow points to ventral tibial apophysis. **d.** *Anachemmis sober* Chamberlin. Arrow points to subtegular/tegular interlocking lobes. C = conductor, E = embolus, MA = median apophysis, RTA = retrolateral tibial apophysis, STP = sclerotized tegular process, Tcb = tegulum at conductor base.

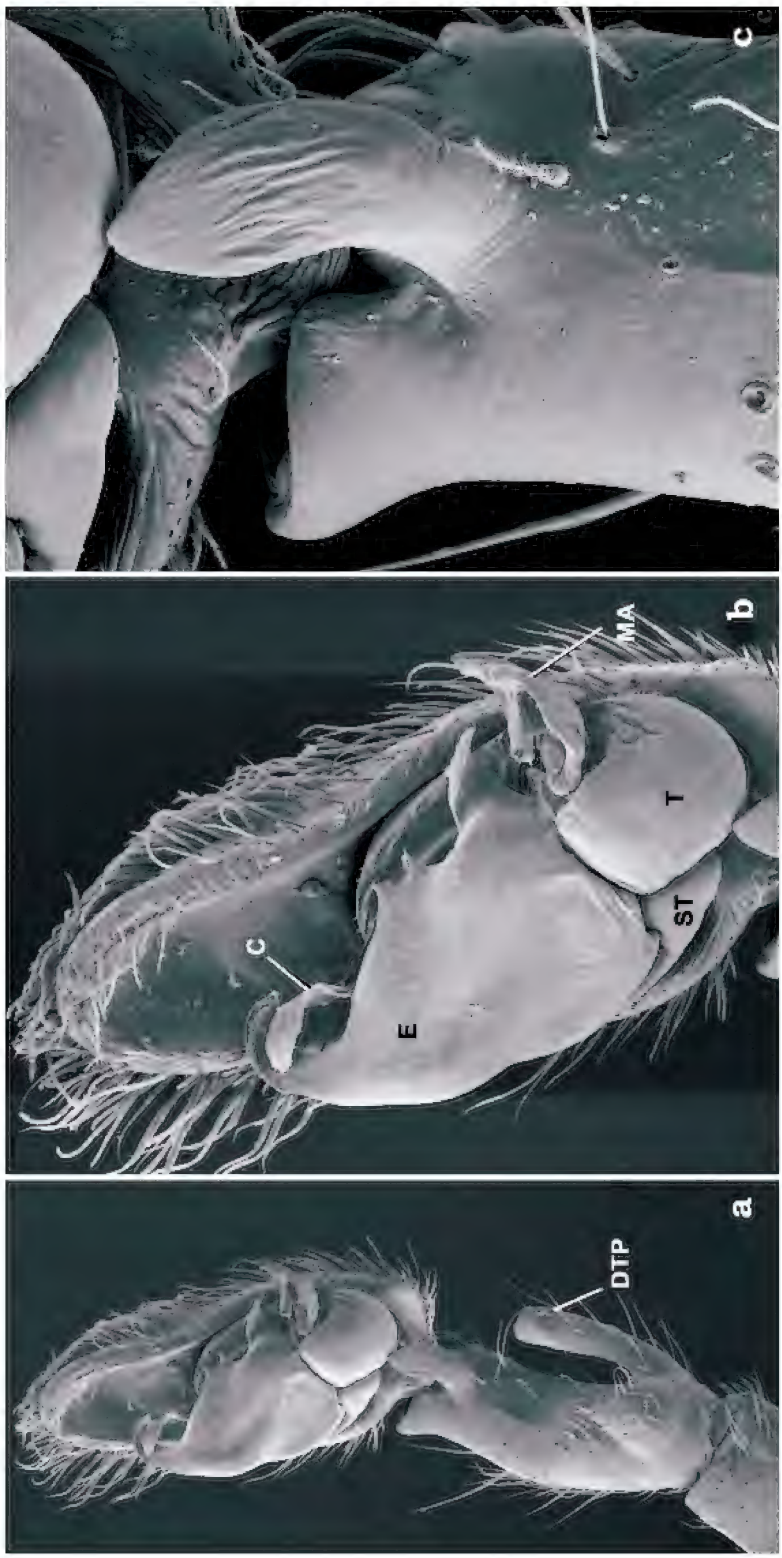

Fig. 14. *Trujillina isolata* (Bryant), left male palp. **a.** Retrolateral view. **b.** Same, closeup of embolus, arrow points to median apophysis. **c.** Same, detail of retrolateral tibial apophysis. C = conductor, DTP = distal tibial process, E = embolus, MA = median apophysis, ST = subtegulum, T = tegulum.

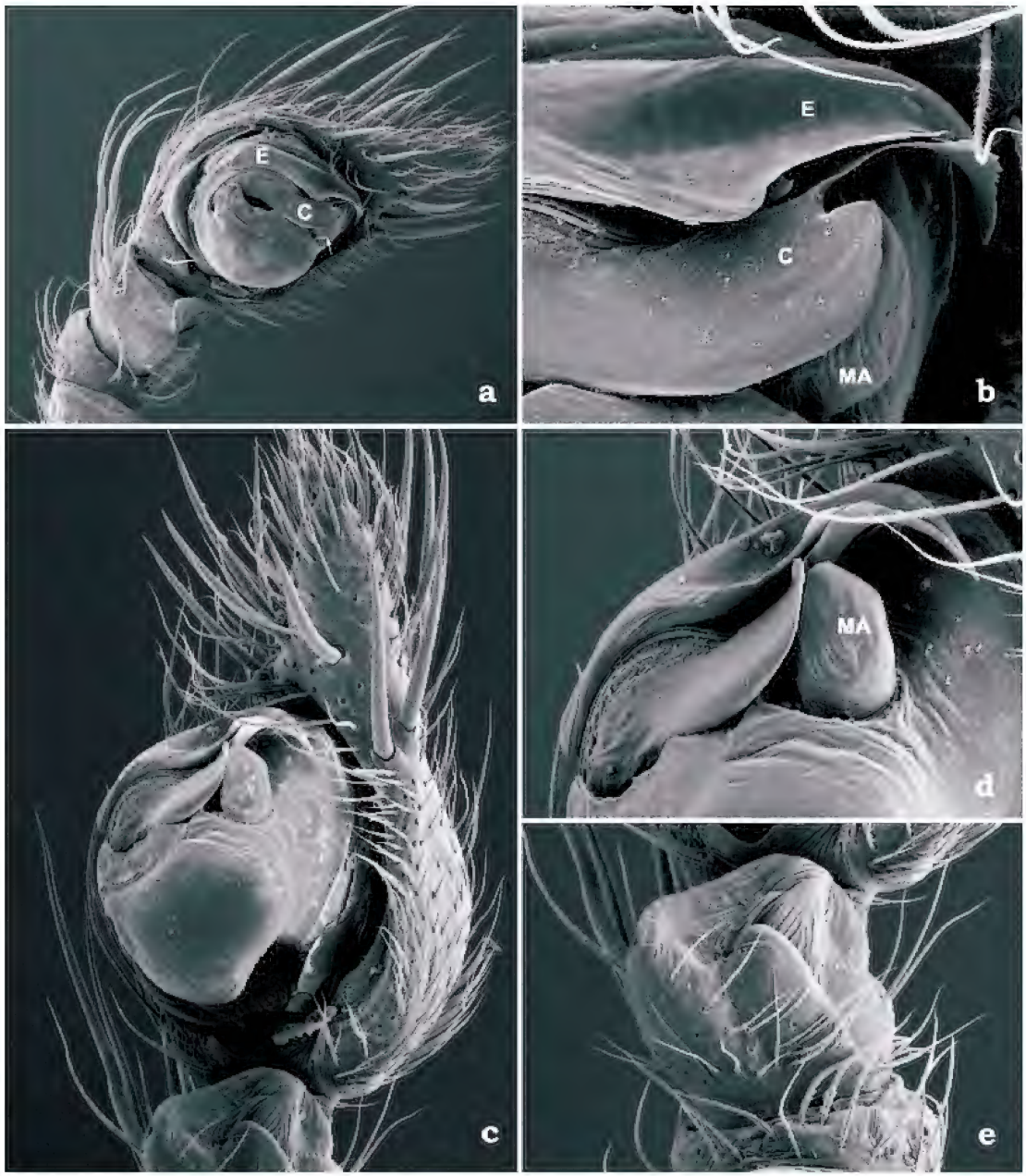

Fig. 15. *Senoculus* sp., left male palp. **a.** Prolateral view. **b.** Same, closeup of lobate conductor and embolus. **c.** Retrolateral view showing large cymbial spines. **d.** Same, closeup of median apophysis and lobate conductor. **e.** Same, closeup of tibia. C = conductor, E = embolus, MA = median apophysis.

Weight = 10, L = 1, CI = 100, RI = 100

Another modification of the male tibiae is shown in *Viridasius*, which has developed at least one subdistal conical process. More often there are three retrolateral processes in adition to the RTA, and their shapes tend to be species-specific.

7. Senoculid tibial projections: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Senoculids differ from all other examined taxa in having a very short, rounded to squared tibia (fig. 15a, e). The palpal tibia is often excavated

and lacks a RTA; however, it may have one or more blunt projections (e.g., Schiapelli and Gerschman de Pikelin, 1957: figs. 2, 3). These kinds of tibial projections are not found in any other examined taxon.

8. Trechaleid tibial indentation (char. 2, Griswold, 1993: fig. 53): absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In trechaleids the tibial apex forms a deep membranous depression (Carico, 1993; Sierwald, 1990, 1993) often surrounded by more complex and sclerotized processes, either retrolaterally as in *Trechalea* (fig. 16c) or ventrally as in *Neoctenus* (fig. 16d). The condition in *Neoctenus* is not entirely well understood, but a coding of either "0" or "1" does not affect its close relationship to the trechaleids. Based on genitalic resemblance, it appears that *Neoctenus* might be most closely related to *Paradossenus* (Brescovit et al., 2000: figs. 1, 2).

9. Tibia apex, sclerotized ring: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The degree of sclerotization of the cuticle around the tibial apex varies across all taxa, but a heavy sclerotization, almost ringlike, is found only in *Caloctenus*.

10. Tibial retroapical notch: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The presence of a deep, hairy fossa at the base of the retrolateral tibial apophysis appears to be restricted to the ctenid genus *Enoploctenus* (Brescovit, personal commun.) but it may as well be a synapomorphy of a more inclusive group within the acantheines. In this matrix, the derived condition was scored for *E. cyclothorax* and *Ctenus miserabilis* Strand. The latter represents a group of species from Ecuador, Peru, and Bolivia. These species may prove to belong at least to one new genus of the acantheine spiders (Silva, personal obs.).

11. Setae crown at tibial apex: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The tibial apex may have ventrally a series of strong, long setae distributed at the same level. This character is seemingly autapomorphic for *Anahita*.

12. RTA (char. 1, Griswold, 1993): absent (0); present (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 57

The presence of a retrolateral process in the male tibia is synapomorphic for a relatively large group of spiders, the so-called "RTA clade" (Coddington and Levi, 1991). The RTA is absent in *Megadictyna*, *Senoculus*, *Psechrus* (fig. 16a), and the lycosids (e.g., *Aglaoctenus*, fig. 16b). A secondary loss of the RTA is one of the synapomorphies for Lycosidae (Dondale, 1986). Some species of *Thalassius* may have a reduced RTA, whereas in some others the RTA is completely lost (Sierwald, 1987), so *Thalassius* is scored "?". A similar kind of variation is observed in an undetermined ctenid species from Africa (Tanzania 1)—some specimens may have only a retrodorsal spine, whereas some others may have a well-developed RTA (fig. 20b), and thus this taxon is scored "0". Within the ctenids the RTA is also lacking in several species of *Anahita*, in *Leptoctenus* ca. *agalenoides*, as well as in some other ctenids from Africa (e.g., *Ctenus auricomus* Arts) and South America (Silva, personal obs.).

13. RTA apical processes: absent (0); with lamella (1); Mad 30-like (2).

Weight = 10, L = 1, CI = 100, RI = 100

Some Indian ctenids (Gravely, 1931) have a lamella arising at the RTA apex (e.g., *Ctenus himalayensis* Gravely, 1931: fig. 1C). The shape of this apical process varies greatly across species and it appears it is easily lost, probably after mating. In some specimens the RTA apical process is broken either in one or both palps. State 2 refers to a presumably autapomorphic condition in a new genus from Madagascar (Mad 30). The RTA in this new taxon greatly narrows to form a neck, and from there it continues as a lanceolate process almost one-half the cymbium length.

14. Leaf-shaped RTA: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The shape of the RTA tends to be autapomorphic either at the generic or species level, although it may also vary within a single species (Höfer et al., 1994: 84). It is not possible to get an accurate coding covering the variation observed across all examined taxa without introducing several autapomorphies. Character 14 refers to a condition observed in *Trujillina*. In this taxon, the RTA is shaped like an elongated leaf (fig. 14c).

15. *Cycloctenus* RTA: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The derived condition refers to a strongly sclerotized RTA shaped in such a way that its base often leads to a kind of smooth ridge from where other processes may arise (e.g., *Cycloctenus westlandicus*; Forster and Blest, 1979: figs. 50, 52). In this dataset, this kind of RTA is present in two of the three species included.

16. RTA basal process: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In all examined Australian zorids—for exam-

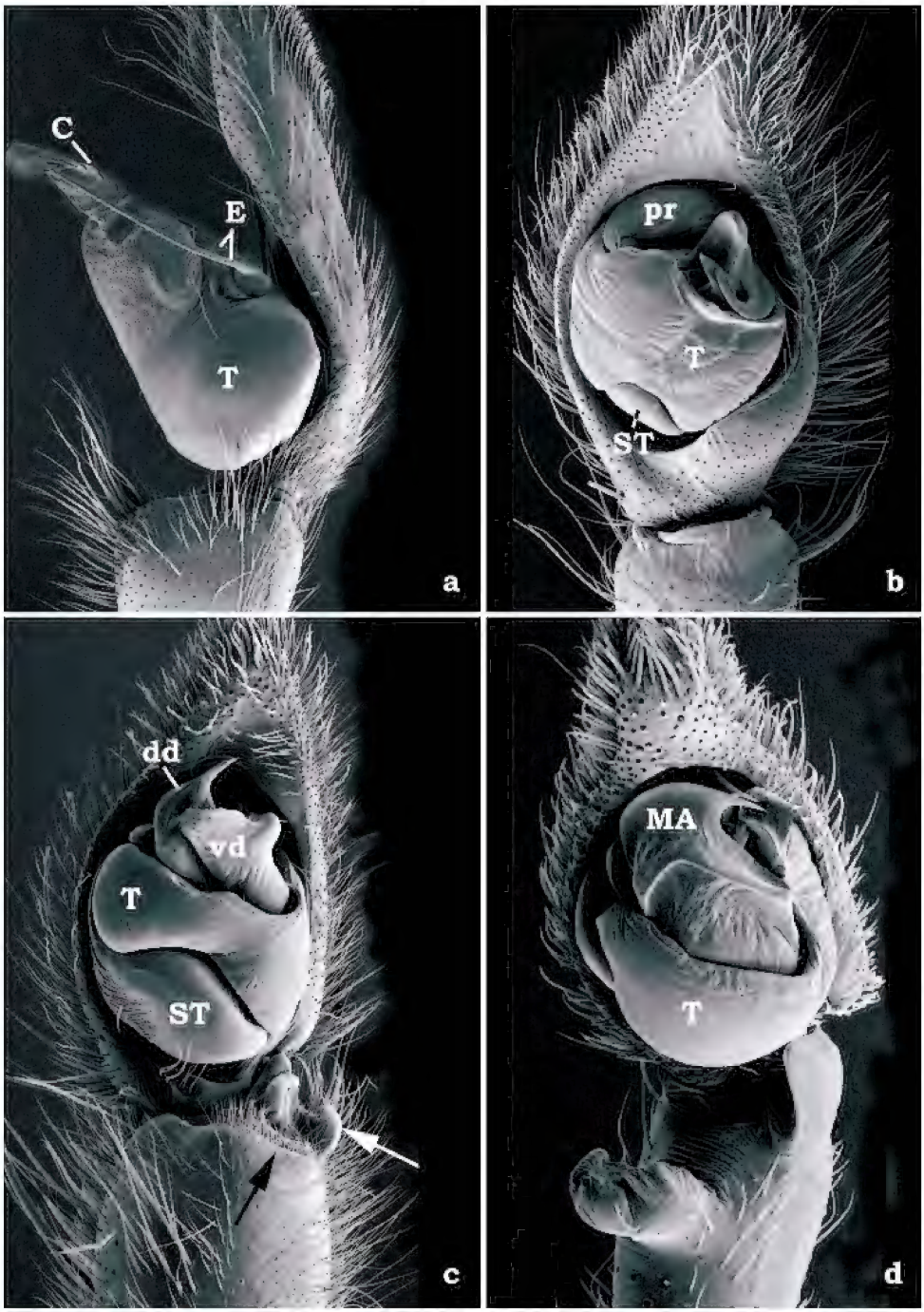

Fig. 16. Left male palp, ventral view. **a.** *Psechrus sinensis* Berland and Berland. **b.** *Porrimosa castaneus* (M.-Leitão.). **c.** *Trechalea connexa* (F.O.P.-Cambridge). **d.** *Neoctenus* ca. *comosus* Simon. Black arrow points to trechaleid tibial rim, white arrow points to retrolateral tibial apophysis (RTA).

ple, *Nemoctenus aurens* (Hogg) (Forster and Wilton, 1973: figs. 1032, 1033) as well as in *Zora* spp. (Heimer and Nentwig, 1991: figs. 1192.1–1197.2b; Roberts, 1995: fig. 37a–d)—there is a distinctive enlargement of the RTA base resembling a kind of transparent wing (fig. 17a).

17. Retrolateral tibial spine: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 57

When the RTA is lacking, the tibia may have one distinctive retroapical spine of variable shape and size. This modified spine has been independently derived in several groups. This spine is often small in *Anahita*, for example in *A. punctulata* (Peck, 1981: fig. 1) and *A. mamma* Karsch (Lessert, 1915: fig. 42). This spine is long and curved in a new species from Chile that is tentatively assigned to *Odo* (fig. 18d). It is spurlike in some species of *Odo* from Central America, but long and straight in at least one species of *Senoculus*.

18. Retroapical tibial spine socket: greatly swollen (0); large (1); small (2).

Weight = 10, L = 2, CI = 100, RI = 100

The spine in *Senoculus* arises from a protruding socket; the spine socket in *Odo* is often round and large (fig. 18d). State 2 refers to a small socket, as is found in almost all examined species of *Anahita* as well as in *Leptoctenus* ca. *agalenoides*.

19. Cymbial trichobothria: present (0); absent (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 88

SEM examination shows that only few of the terminal taxa have retrolateral and/or dorsal cymbial trichobothria. The plesiomorphic condition was scored for the amaurobiids, cycloctenids, clubionids, and also *Apolania*. However, there are a few terminals that still need to be checked for this character.

20. Cymbial spines: none (0); scarce (1); numerous (2).

Weight = 2.6, L = 19 (17 extra steps), CI = 10, RI = 39

21. Cymbial spines: small (0); medium to large (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 80

In most examined taxa as well as in most ctenids the cymbium is completely smooth, but some other taxa may have roughly one to three small spines either prolaterally or apically. In contrast, the cymbium in *Cycloctenus* and *Senoculus* has several medium to large spines covering the cymbium almost entirely (fig. 15a, c).

22. Cymbial retrolateral groove: absent (0); present (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 85

Most examined taxa have the retrolateral cymbial edge smooth, while a few others may have it deeply to shallowly grooved. Among the miturgids, this groove may be either short, as in *Miturga* (fig. 17c), or long, as in *Uliodon* (fig. 17b); in both genera it appears to be associated with long, curved macrosetae. A relatively short groove is also present in Australian zorids (fig. 17a) as well as in *Zora*. Among the ctenids, a long and broad retrolateral groove is present in *Gephyroctenus*.

23. Cymbial groove macrosetae: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In both *Miturga* and *Uliodon* there are very long, curved macrosetae along the cymbial groove (e.g., fig. 17b). Such macrosetae are also found in some undetermined species tentatively assigned to *Argoctenus* but not included in this dataset. These macrosetae are lacking in all examined species of *Gephyroctenus*.

24. Probasal cymbial process: unmodified (0); *Viridasius*-like (1), *Thoriosa*-like (2), *Caloctenus*-like (3).

Weight = 10, L = 3, CI = 100, RI = 100

In most examined taxa the cymbial promargin at its most distal edge is smoothly rounded. State 1 refers to a cymbium projecting into a distal lobate process, as in *Viridasius* (fig. 19a) and most species of *Vulsor*. The condition in state 2 is a cymbium forming a basal spurlike process, as in *Thoriosa* (Benoit, 1976: figs. 7, 10) and a new Australian genus (Raven et al., 2001: fig. 30c). State 3 refers to a short, rounded lobe projecting outward near the base of the cymbium of *Caloctenus gracilitarsis*. Although autapomorphic in this dataset, state 3 is one of the synapomorphies supporting a sister-group relationship between *C. gracilitarsis* and *C. aculeatus* Keyserling, the type species.

25. Cymbial retromargin, basal edge: normal (0); *Acanthoctenus*-like (1); *Vulsor*-like (2); *Trujillina*-like (3); *Thoriosa*-like (4).

Weight = 10, L = 5, CI = 100, RI = 100

In various taxa, the cymbial retromargin may be smooth or it may have a broad range of variation. These cymbial changes represent in many cases species autapomorphies and sometimes apomorphies at suprageneric or generic levels. Character 25 refers only to the changes involving the basal edge of the cymbial retromargin. State 1 refers to the cymbial process observed in the acanthoctenines (fig. 19c, d). State 2 refers to the lo-

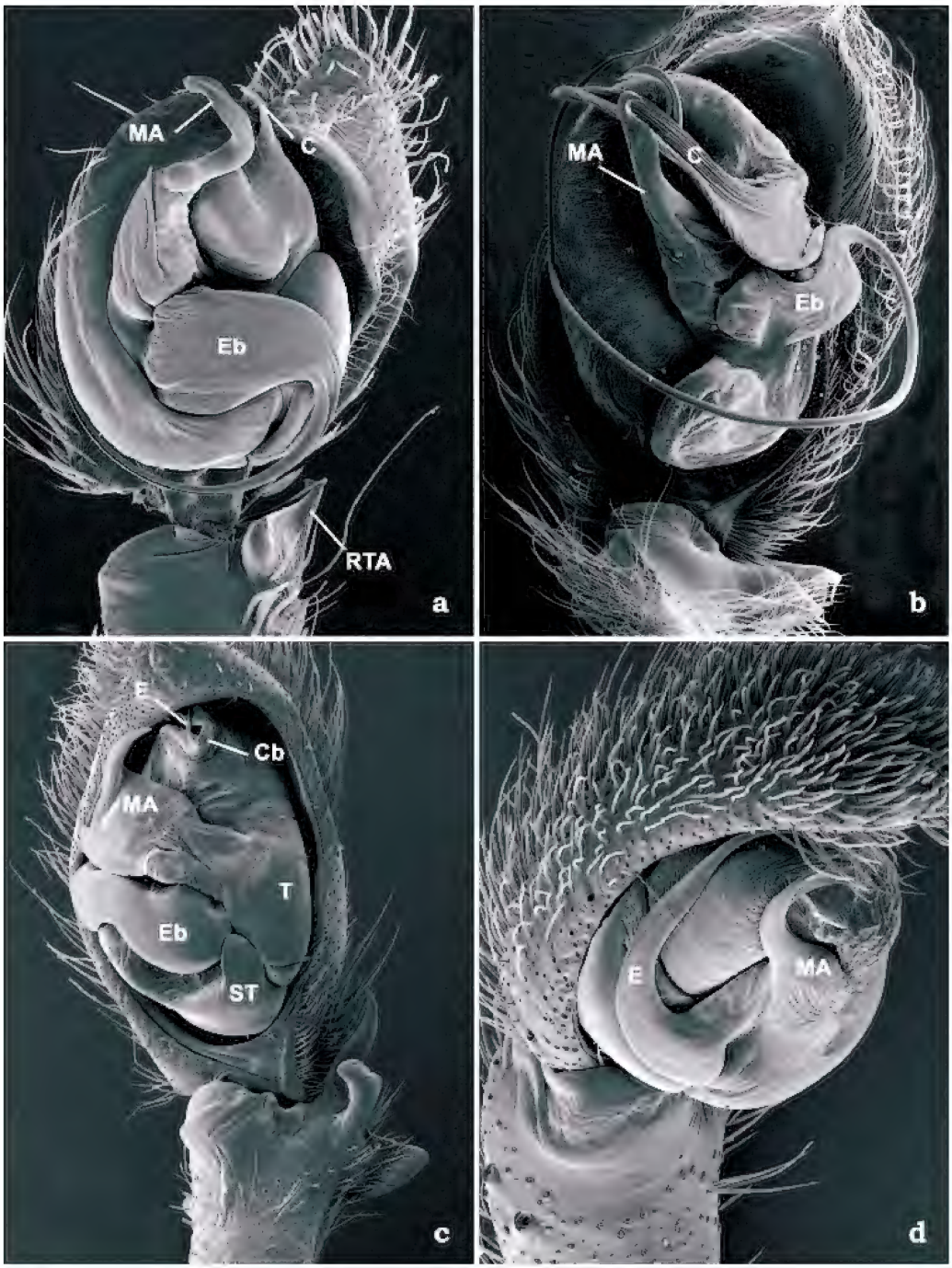

Fig. 17. Left male palp. **a.** *Hestimodema* sp. **b.** *Uliodon tarantulinus* (L. Koch), ventral view. **c.** *Miturga lineata* Thorell, ventral view. **d.** *Teminius affinis* Banks, prolateral view. Arrow points to basal process of retrolateral tibial apophysis. C = conductor, Cb = conductor base, E = embolus, Eb = embolic base, MA = median apophysis.

Fig. 18. Left male palp. **a.** *Odo* cf. *agilis* Simon, ventral view. **b.** *Odo* ca. *lycosoides* (Chamberlin), ventral view. **c.** Same, prolateral view showing an enlarged embolic base between subtegulum and tegulum **d.** *Odo* Chile, retrolateral view. C = conductor, Cb = conductor base, E = embolus, MA = median apophysis, ST = subtegulum, STP = sclerotized tegular process, T = tegulum.

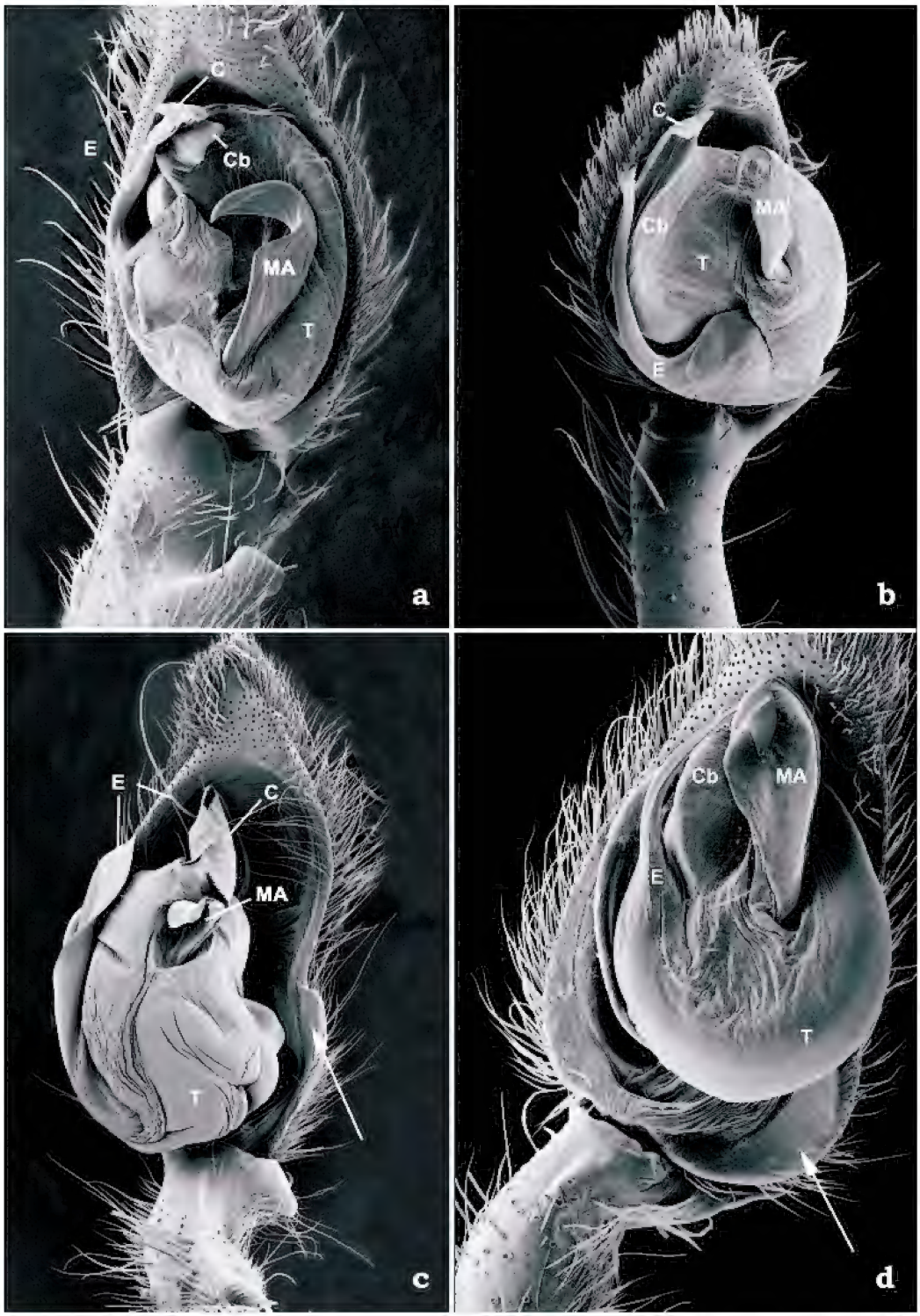

Fig. 19. Left male palp, ventral view. **a.** *Viridasius* ca. *pulchripes* Simon. **b.** Viridasine, Madagascar 2. **c.** *Nothroctenus* cf. *marshii* (F.O.P.-Cambridge). **d.** *Acanthoctenus spiniger* Keyserling. Arrow points to retrolateral cymbial process. C = conductor, Cb = conductor base, E = embolus, MA = median apophysis.

bate process found in most species of *Vulsor*. State 3 (fig. 14a) is a derived condition shared by at least two species of *Trujillina*. State 4 (Benoit, 1976: figs. 7, 10) is an apomorphy shared by all known species of *Thoriosa*.

26. Ventral cymbial process: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

All examined species of *Africactenus* have a large, ventral prong at the base of the cymbium (e.g., Jocqué and Steyn, 1997: fig. 7). This kind of cymbial process is shared with *Petaloctenus bossema* Jocqué and Steyn.

27. Embolus promargin, basal edge: smooth (0); *Odo*-like (1); tengellid-like (2).

Weight = 5.0, L = 8 (6 extra steps), CI = 25, RI = 83

Initially this character was intended to test for the promarginal tegular lobe, which interlocks with a corresponding lobe in the subtegular retromargin, both well developed and clearly seen in the unexpanded palp (Griswold, 1993: char. 6, figs. 9, 19, 25). Although a comparison across taxa showed the occurrence of this lobe, there is a different interpretation about its origin, which was corroborated by examining expanded palps. When present, instead of arising from the tegulum, the interlocking lobe originates directly from the embolus (e.g., fig. 13d). State 1 is an independent transformation of the embolic basal promargin which is greatly enlarged and extends between the tegulum and the subtegulum (fig. 18c); this condition is shared by *Odo* ca. *lycosoides* and *Xenoctenus* ca. *marmoratus*. State 2, properly Griswold's character 6 (i.e., a large lobe or hooklike process; e.g., fig. 13b), is a condition scored for the tengellids (fig. 13d), zorocratids, zoropsids, phanoteans, and some ctenids (e.g., fig. 20a). However, there are still missing entries due to uncertainty in coding the embolic condition in some other ctenids. These problematic taxa either have a rather small lobe, only visible after expanding the palp (e.g., fig. 20b), or they have developed a different kind of pro-basal embolic process (e.g., fig. 20d).

28. Subtegulum retromargin, basal edge: smooth (0); cup-shaped (1); condylelike (2); lobelike (3); *Xenoctenus*-like (4).

Weight = 3.5, L = 15 (11 extra steps), CI = 26, RI = 76

As for the previous character, the great variation observed mainly within ctenids made it very difficult to get an accurate coding. Also, as above, there are still missing entries due to uncertainty in defining the condition in certain taxa.

The plesiomorphic condition is a subtegulum lacking any kind of retro-basal processes (e.g., fig. 16c). State 1 refers to a subtegulum ending in a kind of lobate process that is shallowly excavated (e.g., fig. 14b); this condition is present in *Trujillina isolata*, *Odo* ca. *agilis*, *Odo* ca. *obscurus*, and some of the ctenids (e.g., *Ctenus villasboasi*, fig. 20d). State 2 refers to a subtegulum projecting into a condyle (e.g., fig. 12a) that is present in *Amaurobius ferox* and the cycloctenids. State 3 corresponds to character 104 in Griswold et al. (1999), that is, a subtegular edge with a lobe or hooklike projection clearly seen in the unexpanded palp (e.g., fig. 13d); it was scored for the tengellids, zorocratids, zoropsids, phanoteans, and some ctenids. State 4 refers to the subtegulum projecting into a process almost parallel to the embolic basal projection (fig. 18c) and seemingly synapomorphic for a clade comprising *Odo* ca. *lycosoides* and *Xenoctenus* ca. *marmoratus*.

29. Lycosid tegular notch (char. 19, Griswold, 1993: 14, fig. 52): absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A tegular U-shaped notch (Sierwald, 1990: figs. 9, 31, 48) makes the subtegulum visible in ventral view (e.g., fig. 16b, c). This tegular notch may be small or large, but its presence is seemingly synapomorphic for the trechaleids, pisaurids, and lycosids (Griswold, 1993: 34).

30. Fulcrum: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Sierwald (1990: 22, 39, figs. 5, 6, 8) defined the fulcrum as an apophysis attached to the apical division, more properly, to the distal sclerotized tube which bears the embolus. As it is defined, a fulcrum is scored in this matrix only for *Thalassius* and *Dolomedes*.

31. Pisauridae basal membranous tube (BMT): absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In both *Thalassius* and *Dolomedes* the apical division consists of a membranous inflatable tube connecting the distal tegular projection with the distal sclerotized tube that bears the embolus (Sierwald, 1990: 21, fig. 2). This BMT may prove to be a synapomorphy of Pisauridae (Sierwald, 1990: 37, 45).

32. Pisauridae distal tegular projection (DTP) (char. 20, Griswold, 1993): absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A tegulum projecting into a DTP associated to the apical division (Sierwald, 1990: 21, figs. 5, 7, 8) is a synapomorphy uniting *Dolomedes* and *Thalassius* in this dataset. However, a DTP has been recorded in various pisaurids as well as in other spider groups outside this study (Sierwald, 1990: 43, figs. 16, 22). In some cases (e.g., Sierwald, 1990: fig. 16), the DTP may resemble a

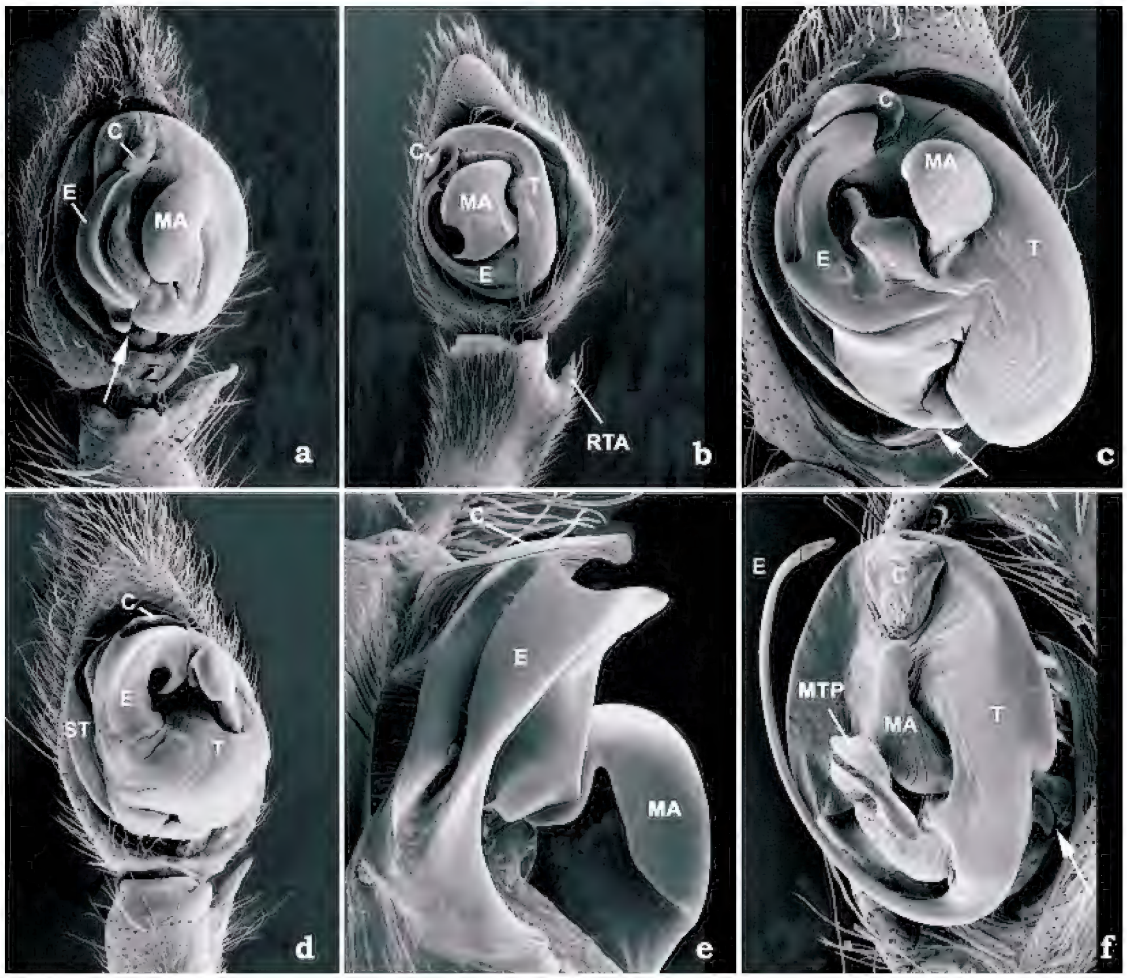

Fig. 20. Left male palp, ventral view. **a.** *Ctenus* cf. *javanus* Pocock. **b.** *Ctenus maculisternis* Strand. **c.** *Ctenus nigrolineatus* Berland. **d.** *Ctenus villasboasi* M.-Leitão. **e.** Same, showing bimarginate median apophysis (MA) and embolus (E), prolateral view. **f.** *Ctenus miserabilis* Strand, retrolateral view showing a membranous tegular process (MTP). White arrow points to subtegulum/embolus interlocking lobes. C = conductor, E = embolus, MA = median apophysis.

tegular process observed in some species of *Vulsor*, but in the latter this projection is closely associated with the base of the conductor rather than with the apical division (Silva, 2001).

33. Ventral tegular indentation: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In ventral view the tegulum may have a deep indentation (fig. 13d). This condition occurs in *Anachemmis* and *Liocranoides*.

34. Tegulum indentation at embolic base: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A prolateral tegular concavity near the embolic base is typical of the palpal structure of *Viridasius* (fig. 19a).

35. Membranous tegular processes (MTP) at embolic base: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 40

In addition to a median apophysis and a conductor, the tegulum may have extrategular processes. These processes may be either membranous or sclerotized. The position of these processes varies widely depending on the species; sometimes they may be associated either with the embolus or the median apophysis.

Membranous processes arising at the embolus

base (e.g., fig. 20f) are variously shaped and are either short or greatly elongated. Although their close association with the embolus may suggest they are part of it (i.e., a modified pars pendula), they are here regarded as independent structures with a tegular origin. MTP processes were scored in *Cycloctenus* ca. *flavus*, *Zorodictyna* sp. (Griswold, 1993: fig. 21), in a new ctenid from Brasil, *Enoploctenus*, *Ctenus miserabilis*, and *Asthenoctenus*.

36. Sclerotized tegular processes (STP) at embolic base (char. 21, Griswold, 1993, figs. 11, 25–27): absent (0); present (1).

Weight = 4.6, L = 8 (7 extra steps), CI = 12, RI = 30

Most examined taxa have an unmodified tegulum near the embolic base, whereas others may have various kinds of sclerotized processes in addition to the median apophysis and the conductor. In order to assess homology of these structures, only those closely associated with the base of the embolus (e.g., fig. 18b) were taken into account. These processes appear to be independently derived in various examined taxa. In this study, they were scored for the zorocratids, some species of *Odo*, and some caloctenine spiders. Although a characteristic STP (Griswold, 1993: figs. 11–14, 25, 26) is thought to be a synapomorphy of Zorocratidae (Griswold et al., 1999), its occurrence appears to be a product of two independent origins. In this study, zorocratids are represented by *Zorocrates* (fig. 13a), *Uduba*, *Zorodictyna*, and *Raecius*. Interestingly, analyses with the zorocratid STP treated as one more character (i.e., "absent"/"present") did not help to group all those taxa in a single clade; the zorocratid STP originated (1) at a node leading to *Tengella*+*Zorocrates* (lost in *Tengella*) and (2) in a clade comprising all other zorocratids (lost in *Zorodictyna*).

37. Proximal tegular process: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A recent revision of Neotropical ctenids showed various species of *Ctenus* with a tegulum projecting proximally (Höfer et al., 1994: fig. 6a, b). A similar configuration is observed in other undetermined species from Central and South America. Among this group of species with proximal tegular processes is *Oligoctenus ornatus* (Keyserling) (Bücherl et al., 1964: fig. 4b), the type species of this genus (holotype examined by Simó, unpub. notes). In this study, proximal tegular processes are scored for *O. ornatus* and an undetermined species from Panama close to *O. medius* (Keyserling).

38. *Odo*-like STP: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

This character refers to a fairly distinctive tegular process, which nearly extends to the embolic apex (e.g., fig. 18a). It is observed in *Xenoctenus* ca. *marmoratus* and a group of species either close to *Odo agilis* Simon (presumably congeneric with the type species) or assigned to *Odo* by various authors.

39. *Hestimodema*-like STP: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A spinelike sclerotized process arising at the median apophysis base (e.g., fig. 17a) appears to be a derived condition of some Australasian zorids, but an in-depth taxonomic revision is necessary to determine if this is an autapomorphy of *Hestimodema* (e.g., Lehtinen, 1967: fig. 400) or a synapomorphy shared with some other zorid species (personal obs.).

40. Tegular process at the conductor base: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 62

In some of the examined taxa, the conductor arises from a tegular projection, which may be slightly modified (e.g., fig 13b; Griswold, 1991: fig. 58) or strongly modified as in *Pimus* and most Malagasy ctenids (e.g., fig. 19a, b). All these processes appear to arise independently several times, and their shapes tend to be diagnostic at the generic level.

41. Tegular processes at conductor base: *Pimus*-like (0); *acaenata*-like (1) (fig. 13b); *Vulsor*-like (2) (Ono, 1993: figs. 2–4); *Viridasius* type (3) (fig. 19a); Madagascar 2 type (4) (fig. 19b); *marshii* type (5) (fig. 19c).

Weight = 10, L = 1, CI = 100, RI = 100

42. Conductor: hyaline or translucent (0); partly sclerotized (1); sclerotized (2); absent (3).

Weight = 4.6, L = 10 (7 extra steps), CI = 30, RI = 30

In this study, a conductor is a name given to a tegular structure arising often at the retroapex from a hyaline rigid base and that may or may not support the embolus. In some taxa, especially lycosids and some pisaurids (Sierwald, 1990: 21), the conductor is a tegular outgrowth lacking articulations of any sort (i.e., completely sclerotized), and recognized as such only by reference to its association with the embolic apex (Griswold, 1993: fig. 59; Sierwald, 1990: figs. 7, 45).

The shape and size of the conductor varies broadly among all examined families and even genera. State 0 refers to a hyaline, flexible structure (e.g., fig. 13d); this condition is present in most examined taxa (e.g., *Dolomedes* and *Thal-*

assius; Sierwald, 1990: 37, figs. 5, 9). State 0 refers also to a conductor that is translucent and more rigid, such as that found in *Cupiennius salei* or some species of *Acantheis*. Since both conditions may occur within a single genus, for the purpose of this analysis they were treated as a single state.

State 2 refers to a conductor that is partly hyaline and partly sclerotized but always has a hyaline base; for example, that in *Amaurobius ferox* (fig. 12a), some psechrids, and some ctenids. *Ancylometes* has a conductor almost completely sclerotized, but it also has a hyaline base and a narrow hyaline apical flange and therefore was scored "1". In *Megadictyna*, the conductor was regarded as present and scored "2", however; the sclerite arising at the embolic base (Harvey, 1995: fig. 195) might correspond instead to the median apophysis (Coddington, 1990: fig. 31). In *Uduba* the conductor is regarded as lacking (Griswold, 1993), but there is an apical sclerotized tegular projection with an enlarged hyaline base supporting the embolic tip (Griswold, 1993: figs. 13, 14), and so this genus was scored as having state 2.

State 3 refers to a completely sclerotized conductor as occurs in the lycosids, for example, *Aglaoctenus* (fig. 16b).

The conductor is secondarily lost in *Trechalea* (fig. 16c) and *Anahita*. The latter genus shows a transformation from a more or less well-developed conductor (e.g., in a new species from New Caledonia), to a reduced narrow "flange" (e.g., in *A. fauna* Karsch, 1879 and *A. punctulata* (Hentz, 1844)) (Peck, 1981: fig. 1), to a complete loss in several species from Asia and Africa (e.g., *Anahita mamma* Karsch, 1884) (Lessert, 1915: fig. 41).

43. Lobate conductor: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A sister-group relationship between the oxyopid *Tapinillus* and *Senoculus* is supported among other characters by the presence of a peculiar conductor (Griswold, 1993: 32, char. 11). The derived condition refers to a conductor sclerotized toward the apex, with a fleshy, rigid attachment to the tegulum and a deep furrow embracing the embolus (fig. 15b–d). Position and function suggest this sclerite is indeed homologous to the conductor found in all other examined taxa. The derived condition is observed also in *Peucetia viridans* (Brady, 1964: fig. 161). This type of conductor has originated independently in *Stiphidion* (Griswold, 1993; Griswold et al., 1999).

44. Median apophysis (MA): absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 0

In this study, a MA is recognized as a tegular sclerite arising either near the center or near the base of the tegulum, but, most importantly, it is articulated to the tegulum through a flexible membrane (Griswold, 1993: 11, figs. 11, 13, 20; Sierwald, 1990: 21; Lehtinen, 1967: 295). A MA is absent in *Megadictyna*, *Clubiona*, *Zoroides*, *Psechrus*, and a new Malagasy ctenid (Mad 30).

45. MA position: opposite embolus (0); at embolic base (1).

Weight = 10, L = 1, CI = 100, RI = 100

In most examined taxa, the MA faces the embolic base (e.g., fig. 12a). By contrast, in *Zora*, the Australian zorids, *Miturga*, *Uliodon*, and *Teminius*, the MA arises practically on top of the embolic base (fig. 17a–d).

46. MA structure: simple (0); complex (1).

Weight = 10, L = 1, CI = 100, RI = 100

The shape of the MA often suggests a synapomorphy at the generic level (Sierwald, 1990: 37), and that is the case for many of the examined taxa. Character 45 refers only to the condition observed among some trechaleids (Carico, 1993: 235, figs. 15–24). In both *Trechalea* and *Neoctenus*, the MA is a rather large, bulky sclerite divided into a ventral and a dorsal branch (fig. 16b, c).

47. Cup-shaped MA: absent (0); present (1).

Weight = 7.5, L = 3 (2 extra steps), CI = 33, RI = 91

A cup-shaped MA is a synapomorphy supporting the monophyly of the "ctenoids" sensu Griswold (1993: 30, char. 14). A cup-shaped MA is recognized by having an excavated ventral surface with a convex dorsal edge (e.g., fig. 20d). This type of MA may in turn be variously shaped (e.g., figs. 13b, 20a–f). The derived condition was scored for *Griswoldia*, *Phanotea*, some ctenines, and some acantheines.

48. Cup-shaped bimarginate MA: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

A cup-shaped MA split at the apex (e.g., fig. 20e) is referred to as bimarginate (Griswold, 1993: fig. 8, char. 15). The derived condition is scored for *Griswoldia* and *Phanotea* as well as some ctenine spiders (e.g., *Oligoctenus*, *Phoneutria*, and *Isoctenus*). This character is inapplicable for most examined taxa.

49. *Titiotus* MA: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Some of the examined tengellids share a very similar male palpal structure; here, these similarities are represented by their peculiar apically split MA (fig. 13c), which may prove to be a synapomorphy for a more inclusive group (Platnick, 1999: 4). The slightly bifid MA in *Zoropsis rufi-*

pes (e.g., Levy, 1990: fig. 18) as well as the strongly bifurcated MA in *Gephyroctenus* are seemingly not homologous to the condition observed in *Titiotus* and therefore they are scored "0".

50. Embolus origin: retrolateral (0); median (1); prolateral (2); apical (3); proximal (4).

Weight = 3.7, L = 14 (10 extra steps), CI = 28, RI = 52

The origin of the embolus may vary within a single genus. For example, it arises retrolaterally in many species of *Vulsor* (e.g., Ono, 1993: fig. 2), whereas in some others it may arise proximally or distally (e.g., Ono, 1993: fig. 4). *Anahita* also exhibits variation in the origin of the embolus, either retrolaterally as in *A. punctulata* (Peck, 1981: fig. 2), distally as in the New Caledonian species, or more medially positioned as in some species from Africa (e.g., Benoit, 1977: fig. 1a).

In some other taxa, the origin of the embolus appears to be more stable at the generic level. State 0 is observed in *Megadictyna* (Forster, 1970: fig. 509) and *Gephyroctenus*. State 1, an embolus arising from the center of the tegulum (e.g., fig. 17d), occurs in *Zora*, the Australian zorids, *Miturga*, *Uliodon*, and *Teminius*. State 2, a prolateral origin (fig. 13d), is the condition usually found among the examined taxa. State 3, an apical origin (fig. 16a), is found in *Psechrus*, the pisaurids, the lycosids, and also in all species of *Cupiennius* (Barth and Cordes, 1998: figs. 23–31; Brescovit and Eickstedt, 1995: figs. 1, 7). State 4, a proximal origin (fig. 19b), is found in various ctenids as well as in *Ancylometes*.

51. Embolus shape: spiral (0); coniform (1); lamelliform (2); spinelike (3); coiled (4); ribbonlike (5); *Diallomus* type (6); *Clubiona* type (7); *Trujillina* type (8); *Strotarchus* type (9).

Weight = 2.4, L = 28 (19 extra steps), CI = 32, RI = 52

The embolus varies widely across taxa. Since it is highly species-specific, it is very difficult to classify the various forms into more general types that could indicate something about higher-level relationships. Character 51 is an attempt to classify all the various kinds of emboli observed across the examined taxa according to the work of Comstock (1910: 182, figs. 25.1–25.3); however, there are still missing entries due to uncertainties in coding.

A spiral embolus, that is, a "gutterlike" sclerite often with a well-defined pars pendula and tapering apically (e.g., fig. 13b), is regarded as the plesiomorphic condition among lycosoids (Griswold, 1993: 35). A coniform embolus, that is, one having a broadly expanded base and a nearly straight and narrower apical cone, is scored in *Caloctenus gracilitarsis*, which shares this condition with *Caloctenus aculeatus*. A lamelliform embolus is a flattened, stout sclerite, often more complexly structured (e.g., fig. 13d). The latter type is observed also in various taxa, and within ctenids it is typical of *Viridasius* but it occurs in several other ctenids as well.

With exception of the *Diallomus* type, all other states may be considered as variants of the spiral type. These variations are treated as separate states to emphasize their uniqueness among the examined taxa. State 3 refers to the short, spinelike embolus (e.g., fig. 16a, b) observed primarily among higher lycosoids (*Psechrus* to lycosids), as well as in *Cupiennius*.

State 4, a coiled embolus, is characterized by having a greatly elongated and very thin truncus either hidden behind the tegulum (e.g., in *Zorocrates*; fig. 13a) or encircling the tegulum as is observed in some zorids (e.g., *Hestimodema*; fig. 17a) and some miturgids (e.g., *Uliodon*; fig. 17b); within ctenids, a coiled embolus is typical of such genera as *Gephyroctenus* and *Vulsor*. State 5 refers to the embolus in a group of species close to *Nothroctenus marshii*, which has a broad ribbonlike base tapering into a whiplike apex (fig. 19c). State 6 refers to a different kind of embolus occurring (so far) only in *Diallomus*. States 7 and 9 appear to be autapomorphies for *Clubiona bryantae* and *Strotarchus piscatorius*. On the other hand, state 8 is shared by both species of *Trujillina* (fig. 14b).

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52. Epigynum configuration: anterior and posterior folds (0); median and lateral folds (1); senoculid-like (2); single fold (3).

Weight = 5.4, L = 8 (5 extra steps), CI = 37, RI = 64

Megadictyna and some other outgroups have an epigynum formed by anterior and posterior folds (e.g., *Cycloctenus westlandicus*; Forster and Blest, 1979: fig. 53). State 1 refers to a longitudinal development of the epigynum resulting in median and lateral folds (Sierwald, 1989). These longitudinal foldings may be either well differentiated into median and lateral sectors (fig. 21b), or partly to entirely fused. State 1 is the condition found in various outgroups and several ctenids (e.g., fig. 22d).

State 2 refers to a condition in senoculids, where the epigynum is formed by two separate cuticular hornlike evaginations (fig. 21a). This kind of epigynal development results in each spermatheca being encapsulated inside the protruding

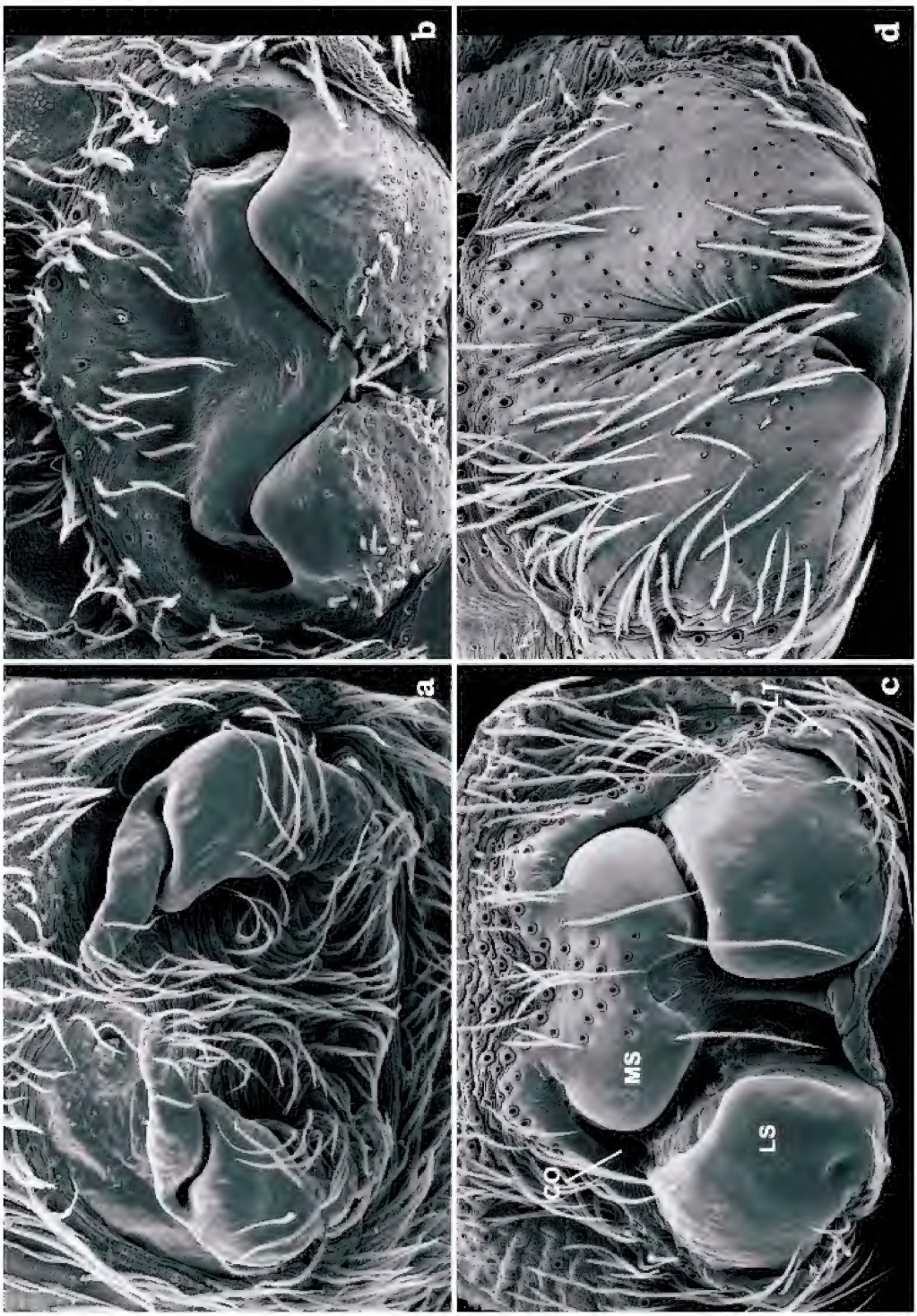

Fig. 21. Epigynal structure, ventral view. **a.** *Senoculus* sp. **b.** *Neoctenus* ca. *comosus* Simon. **c.** *Griswoldia acaenata* (Griswold). **d.** *Odo* cf. *agilis* Simon. CO = copulatory opening, LS = epigynal lateral sector, MS = epigynal median sector.

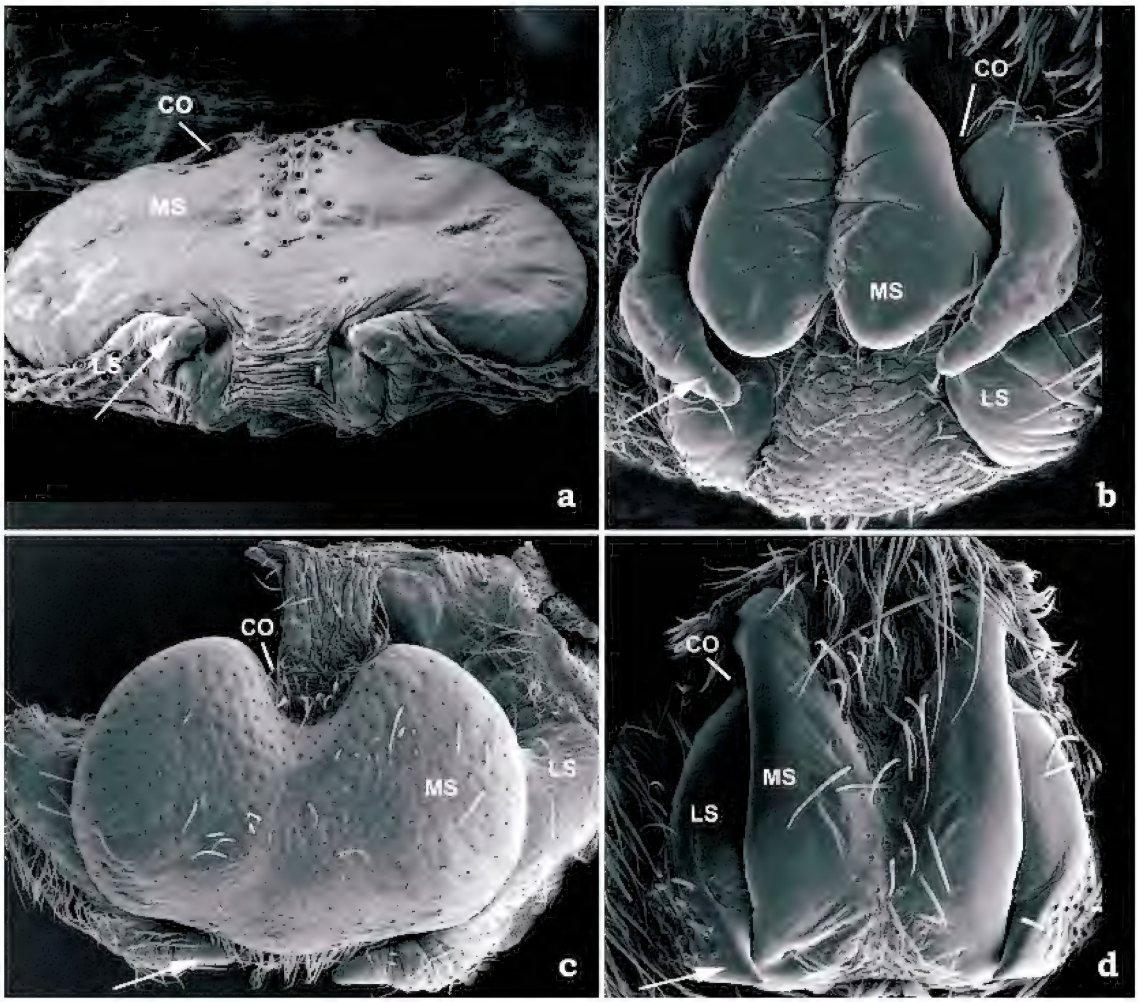

Fig. 22. Epigynal structure of some ctenid spiders. **a.** *Anahita punctulata* (Hentz), posterior view. **b.** *Ctenus villasboasi* M.-Leitão, retromesad view. **c.** *Ctenus inaja* Höfer et al., ventral view. **d.** *Ctenus nigrolineatus* Berland. CO = copulatory opening, LS = epigynal lateral sector, MS = epigynal median sector. Arrow points to LS tooth.

horn (e.g., Schiapelli and Gerschman de Pikelin, 1957: fig. 1; Chickering, 1941: fig. 3).

State 3 refers to an epigynal cuticle apparently undifferentiated, either lightly sclerotized or not sclerotized at all, and therefore allowing a clear view of the internal genitalia (e.g., fig. 23c). This condition is observed in some outgroups, especially *Zora* and closely related genera, and it is also more often seen in most caloctenines (e.g., a new species of *Caloctenus* from Peru). In this genus, there is a transformation from well-developed, strongly sclerotized lateral and median sectors (e.g., *Caloctenus aculeatus* Keyserling) to epigynal foldings that are partly (e.g., *C. gracilitarsis* Simon) or entirely fused and transparent (e.g., a new species from Peru).

53. Epigynal lateral sectors *Odo*-like: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In some species assigned to *Odo* and *Xenoctenus* the epigynal lateral sectors are projecting posteriorly into membranous, often pocketlike, lobes (fig. 21d).

54. Epigynal alveoli: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In some taxa the copulatory openings are marked by whitish, roughly oval-shaped alveoli.

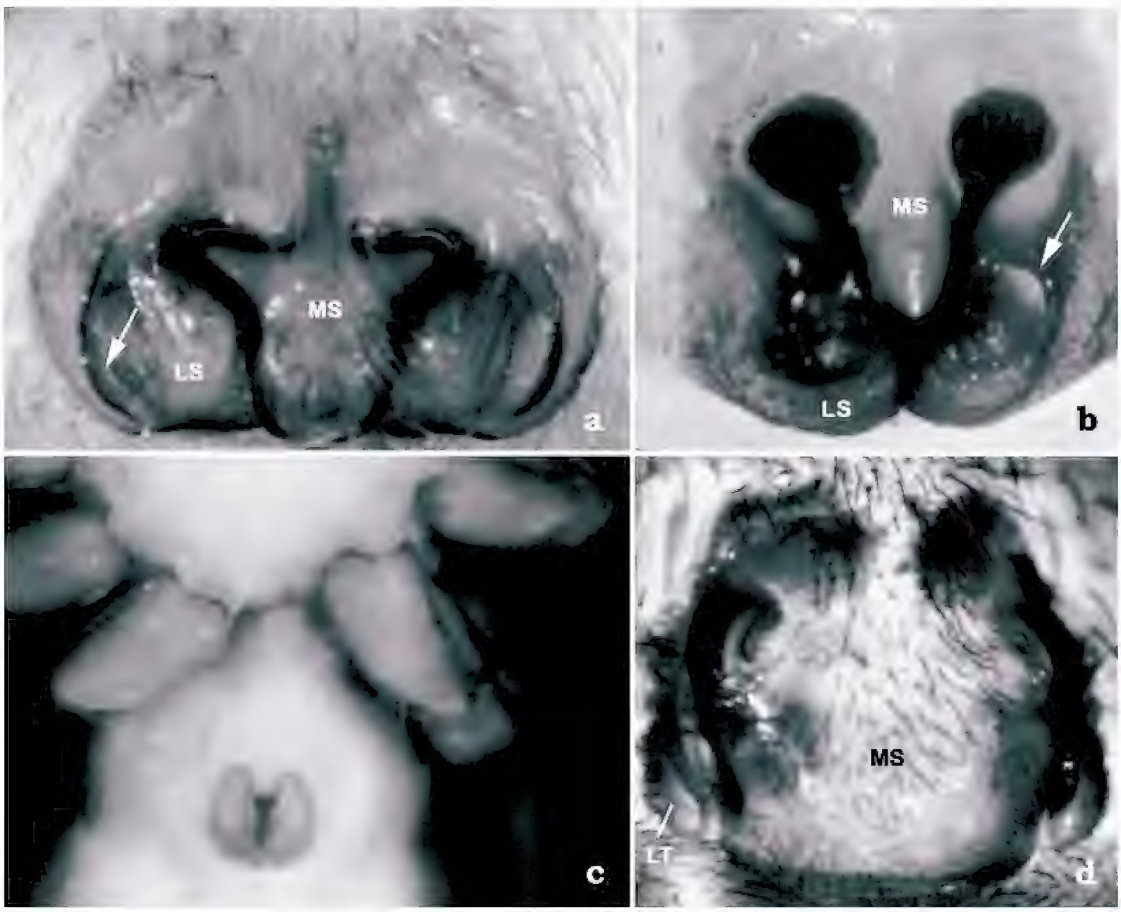

Fig. 23. Epigyna of selected terminals, ventral view. **a.** *Zoropsis rufipes* (Lucas), arrow points to pocket in lateral sector. **b.** *Viridasius* sp., arrow points to sclerotized ledge in lateral sector. **c.** *Diallomus* sp., ventral view showing internal genitalia through epigynal cuticle. **d.** Peru 1, ventral view showing sclerotized median plate. LS = epigynal lateral sector, MS = epigynal median sector, LT = LS tooth.

This kind of hyaline cuticle is present in most examined species of *Anahita* (Benoit, 1977: 369, fig. 2b; Bristowe, 1931: fig. 5); one of the exceptions is *A. punctulata*, where these alveoli are not well marked (Peck, 1981: fig. 3). The epigynal alveoli are also scored in *Leptoctenus* nr. *agalenoides* and in a new species (Australia 15) closely related to *Janusia* (e.g., see Gray and Thompson, 2001: fig 3d, e).

Copulatory openings marked by hyaline cuticle variously shaped may occur in some *Acantheis*, as well as in some other ctenids, e.g., *Cupiennius* spp. (Barth and Cordes, 1998: fig. 14, Brescovit and Eickstedt, 1995: fig. 3) and *Ctenus sinuatipes* (F.O.P-Cambridge, 1897a: pl. III, fig. 4d). However, the origins of these markings are rather different in each taxon, and therefore they are not regarded as being homologous to the condition in *Anahita*.

55. Median sector sclerotized plate: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 85

The epigynal median folding varies widely across taxa, but in *Titiotus* and various ctenids it is differentiated into a strongly sclerotized, broad plate (e.g., fig. 22c). With the exclusion of *Ctenus* (a polyphyletic taxon, fig. 22b–d), the shape of the epigynal median sector plate is often diagnostic at the generic level. However, its presence also might help in defining a more inclusive group within ctenids.

56. Lateral sector processes: absent (0); present (1).

Weight =5.4, L = 6 (5 extra steps), CI = 16, RI = 86

The epigynal lateral foldings may be entirely

smooth (fig. 21b), they may have some kind of cuticular outgrowths, partly membranous and pocketlike (fig. 23a) or strongly sclerotized and hoodlike (fig. 23b), or they may have many other kinds of strongly sclerotized apophyses.

57. Lateral sector apophyses: *Odo patricius* type (0); *Uliodon* type (1); toothlike (2); *Isoctenus* type (3); *Viridasius pulchripes* type (4); *Viridasius fasciatus* type (5); short lobes (6); bifid (7).

Weight = 8.5, L = 8 (1 extra step), CI = 87, RI = 75

The shape of the lateral sector apophyses varies greatly and it is often species-specific. Although the position of these apophyses may be more informative at the generic level, the variation observed across taxa is still rather difficult to homologize, especially when referring to the "toothlike" type.

State 0 refers to greatly swollen lateral projections, seemingly autapomorphic for *Odo patricius*. State 1 refers to the condition observed in *Uliodon*, which has the epigynal lateral sector projecting apically into a squarish, short process (Griswold, 1993: fig. 48). State 2 refers to a toothlike process (e.g., fig. 21c), that is, short and pointed, as in *Griswoldia* and various ctenids (e.g., fig. 22d). These lateral teeth may also be rather long and blunt, as in *Phanotea* (Griswold, 1994: fig. 45), and this condition is also found in various ctenids (e.g., *Ctenus villasboasi*; fig. 22b).

State 3 refers to very short, blunt, apical projections of the epigynal lateral sector; this condition occurs in a group of species closely related to *Isoctenus coxalis*. States 4 and 5 refer to putative synapomorphies of species groups closely related to *Viridasius pulchripes* and *V. fasciatus*, respectively (Silva, 2001). State 6 refers to epigynal LS projecting into posterior fingerlike processes (e.g., fig. 22a); these processes were found in some species of *Anahita*, in *Leptoctenus* nr. *agalenoides*, and in *Janusia*. State 7 appears to be autapomorphic for *Ctenus narashinai*, which has epigynal lateral sectors with broad, bifid projections (Patel and Reddy, 1988: fig.2c, d).

58. Lateral sector pockets: absent (0); present (1).

Weight = 7.5, L = 3 (2 extra steps), CI = 33, RI = 50

These pocketlike structures are bordering shallow lateral sector depressions and are lightly sclerotized (e.g., fig. 23a). They were scored for *Tengella*, *Anachemmis*, *Uduba* (Griswold, 1993: fig. 15), *Zorocrates*, and *Zoropsis*.

59. Lateral sector hoodlike structures: absent (0); present (1)

Weight =8.5, L = 2 (1 extra step), CI = 50, RI = 50

This character refers to strongly sclerotized, blind cuticular slits with a dorsal hood (e.g. fig. 23b) that extend internally into large apodemes. The derived condition is characteristic of some viridasine spiders.

60. Epigynal sulci: not conspicuous (0); clearly marked (1).

Weight = 7.5, L = 3 (2 extra steps), CI = 33, RI = 50

In ventral view the epigynal fold is seen to form a sulcus between the median and lateral sectors (e.g., fig. 21c). This sulcus (often filled with a dark secretion) is observed in such taxa as *Phanotea* (Griswold, 1994: figs, 7, 61), *Griswoldia* (e.g., fig. 21c), and within ctenids in some of the viridasines (e.g., see fig. 32b).

61. *Phanotea*-like, S configuration: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 50

In *Phanotea*, the epigynal fold appears internally as a strongly sclerotized structure containing the copulatory ducts and distally separating the head from the base of the spermathecae (Griswold, 1994: figs. 6, 48). This condition is present in a new Chilean species, in some species of Viridasiinae, and also in *Asthenoctenus* (Simó and Eickstedt, 1994: figs. 4, 5).

62. Spermathecal loop: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In *Janusia muiri* each spermatheca is surrounded by a strongly sclerotized "loop"; additionally, the copulatory ducts form a membranous and narrow loop before entering the spermathecae close to the fertilization ducts (Gray, 1973: fig. 4). A similar condition is observed in a new species (Australia 5) here assigned to *Janusia*.

63. Secondary receptacle: absent (0); present (1).

Weight = 6.0, L = 5 (4 extra steps), CI = 20, RI = 42

In lycosids and trechaleids (e.g., Carico, 1993: fig. 10) there is an enlargement of the spermatheca base, forming a bulbous structure. This lobate structure is considered a synapomorphy supporting a sister group relationship of the Lycosidae and Trechaleidae (Griswold, 1993: 34). A similar process appears to be independently derived in *Cupiennius*, where there is a rounded enlargement behind the base of each spermatheca. This structure is thought to be a secondary spermatheca (Barth and Cordes, 1998: fig. 16; Lachmuth et al., 1984; Melchers, 1963: 24, fig. 12). Another independent origin occurs in *Enoploctenus*, which also has a well-differentiated lobate process at the base of the spermathecae.

64. *Vulsor*-type copulatory ducts: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Among ctenid spiders, *Vulsor* is distinguished by a long copulatory duct divided into two regions: a median branch, strongly sclerotized, and a lateral branch, often membranous and spiralling around the spermatheca (Silva, 2001). Copulatory ducts, long, membranous, and forming spirals, are observed in various taxa outside this study, for example among phyxelidid spiders (Griswold, 1990: fig. 64a), but they lack the median branch.

CARAPACE

65. Caput: normal (0); slanting forward (1).

Weight = 10, L = 2, CI = 100, RI = 100

A caput strongly projecting forward (e.g., fig. 26b) is a distinctive feature of the senoculids.

66. Pars cephalica: inconspicuous (0); strongly marked (1).

Weight = 10, L = 1, CI = 100, RI = 100

In some species of *Cycloctenus* (e.g., *C. westlandicus*), the pars cephalica is marked by deep and broad cephalic furrows (Forster and Blest, 1979: figs. 32, 38). In *Megadictyna* the pars cephalica is also well marked, but in this case it is due to the prominent endocephalic venom glands and is therefore not considered a homologous condition.

67. Carapace profile: convex (0); broadly indented (1); amaurobiid-shaped (2); *Uduba* type (3); senoculiid-shaped (4); V-shaped (5).

Weight = 8.5, L = 6 (1 extra step), CI = 83, RI = 93

State 0 refers to a carapace either uniformly raised or higher at the thoracic fovea, which is the condition in most examined taxa. State 1, a broadly indented carapace, characterizes some of the cycloctenids (e.g., Forster and Blest, 1979: fig. 32). Although *Megadictyna* was scored "1", the condition is probably not homologous, but coding both families as "1" or "0" does not affect the results.

State 2 refers to the raised carapace in both *Amaurobius* and *Pimus*. State 3 resembles the condition in amaurobiids, but here the carapace extends posteriorly and it is more flattened. State 4 is a unique condition observed in *Senoculus*, which has a thin, flattened, and elongated profile. State 5 refers to a carapace with a broad pars thoracica, which may be either shallowly or deeply indented at the fovea (e.g., Lehtinen, 1967: fig. 412). This depth variation does not seem to be informative; it occurs randomly in both *Acantheis* and *Enoploctenus* and was finally coded as a single state.

68. Thoracic fovea: ill-defined pit (0); broad slit (1); narrow slit (2); absent (3).

Weight = 5.4, L = 8 (5 extra steps), CI = 37, RI = 28

State 0 represents the condition in *Senoculus*, where there is a kind of ill-defined pit. A longitudinal fovea is found in all other taxa, being either long and broad, as in the amaurobiids and other outgroups, or long and narrow, as in most taxa. The absence of a thoracic fovea is considered a synapomorphy of Eutichurinae (Ramirez et al., 1997: 45); in this matrix, it is also lacking in *Megadictyna* and *Psechrus*.

69. Ocular ridge: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In *Janusia muiri* as well as in the new species here attributed to this genus, there is a transverse ridge on top of the clypeus (Gray, 1973: fig. 1); this ridge is lacking in all of the other blind ctenid species so far examined.

70. Chilum: absent (0); present (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 45

A chilum (Jocqué, 1991: 11) is absent in *Megadictyna*, the cycloctenids (e.g., fig. 24a), *Hestimodema*, *Argoctenus*, *Zora*, *Senoculus*, *Peucetia*, *Liocranum*, and within ctenids in some of the caloctenines. The derived condition is observed in all the other examined taxa.

71. Chilum (char. 37, Griswold et al. 1999): entire (0); divided (1).

Weight = 6.0, L = 5 (4 extra steps), CI = 20, RI = 63

An entire sclerotized plate is found in amaurobiids (e.g., fig. 25a), clubionids, *Strotarchus*, *Eutichurus*, *Teminius*, pisaurids, *Trechalea*, *Xenoctenus*, and *Odo* ca. *lycosoides*. Two sclerotized plates (e.g., fig. 25l) are observed in a great majority of the examined taxa. Occasionally, the chilum is divided only in part (e.g., in *Aglaoctenus*), and therefore this taxon was scored "0" for this character. Although a divided chilum is commonly found among the ctenids, within this family there is a broad range of variation, even at the intraspecific level. For example, some ctenine specimens may have an entire chilum, whereas a few others may have it either partly or entirely divided (e.g., *Phoneutria boliviensis*).

72. Crossing cheliceral spines: absent (0); present (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 0

Most examined species of *Cycloctenus* have two pairs of cheliceral spines crossing the opposite pair (Hickman, 1981: fig. 15). These modified spines (fig. 24a, b) have a rather conspicuous and

Fig. 24. Chelicerae and endites. a, b. *Cycloctenus* sp. **a.** Female chelicerae, dorsal view showing cheliceral spines (chs). **b.** same, closeup of spine base. c–f. Closeup of endites showing serrula. **c.** *Amaurobius ferox* (Walckenaer), female, ventral view. **d.** Same, dorsal view. **e.** Ctenid, n. sp., Indonesia (Lombok), female. **f.** *Acantheis* sp., Malaysia (Sabah), male.

large socket, which is hard to miss even if the spine is lost. In this matrix, the derived condition was scored for *Cycloctenus westlandicus* and *C.* ca. *flavus*.

73. Cheliceral promarginal teeth: 1 (0); 2 (1); 3 (2); 2 or 3 (3); 4 or 5 (4); none (5).

Weight = 10, L = 5, CI = 100, RI = 100

Cheliceral teeth have often been considered important in taxonomic works dealing with various spider families, and ctenids are not an exception. In general, their number and size vary broadly, even from the right to left side in a single speci-

men. Promarginal teeth appear to be more stable than those on the retromargin. However, the presence of denticles (tiny teeth along the same row of larger teeth) makes it harder to use them consistently. This kind of variation is taken into account in characters 73 and 74.

State 0 was arbitrarily chosen for the occurrence of a single tooth; however, this condition appears to be derived in *Megadictyna* (Harvey, 1995: 282), which also lacks denticles. State 0 has been scored also for the two amaurobiids; however, *Pimus napa* has four denticles and no tooth, whereas *Amaurobius ferox* has one tooth and three denticles.

The cycloctenids are a good example of the variation in cheliceral teeth within a single genus (Hickman, 1981: 50). In *Cycloctenus* ca. *flavus* there are two teeth and no denticles (state 1), whereas in the other two species there are four or five teeth, and they may have either one or two additional denticles. State 2 refers to three teeth on the cheliceral promargin (a middle one larger than the other two). This is the condition observed in most of the examined taxa, and only a few of them have additional denticles (e.g., some species assigned to *Odo*, the clubionids, *Zorocrates*, and some ctenids).

State 3 refers to both *Dolomedes* and *Thalassius*, which have either two or three cheliceral teeth. This condition is introduced to point out the variation within a single genus: three or two teeth plus a proximal tiny denticle, which may be lacking in some species of *Thalassius* (Sierwald, 1987: 56, fig. 13). State 4 refers to the presence of either four or five teeth on the promargin; this variation occurs also within a single genus. State 5 refers to the condition in *Peucetia*; although it is also observed in *Tapinillus*, other oxyopids appear to have a single cheliceral tooth (Brady, 1964: 444).

74. Promarginal denticles: absent (0); present (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 33

75. Retromarginal teeth: none or one (0); two (1); three (2); four (3); five (4).

Weight = 2.6, L = 21 (17 extra steps), CI = 19, RI = 73

76. Sternum base: slightly to strongly projected between coxae IV (0); extending to coxae IV (1); not extending to coxae IV (2).

Weight = 3.7, L = 12 (10 extra steps), CI = 16, RI = 80

The sternum broadly separates coxae IV in *Megadictyna*, *Senoculus* and *Peucetia*. Although not so strongly conspicuous, state 0 was scored also for *Liocranum*, *Hestimodema*, *Elassoctenus*, *Argoctenus*, *Psechrus*, *Trechalea*, and the new caloctenine from Madagascar (Mad 30).

Some other taxa may have the sternum extending to coxae IV but not projecting between them. This condition occurs in the lycosids, pisaurids, most tengellids, most udubiids, *Odo* ca. *lycosoides*, the Malagasy ctenids, *Cupiennius*, and in a new species of *Caloctenus*. In all the remaining taxa (e.g., *Liocranoides*, *Zorodictyna*, *Ancylometes*, and a great majority of ctenids), the sternum does not extend to coxae IV.

77. Precoxal sclerites: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

The presence of precoxal sclerites (i.e., the roughly triangular and strongly sclerotized structures between the sternum and the coxae) is considered synapomorphic for a group of spiders including such taxa as clubionids, liocranids, and gnaphosids, and a few others (Platnick, 1990: 35). These sclerites are well developed in the clubionids and *Liocranum*. They are also well developed in the miturgid genera *Eutichurus* and *Strotarchus*. By contrast, *Miturga*, *Uliodon*, and *Teminius* have tiny, lightly sclerotized structures of doubtful homology and are therefore scored "?". However, neither a "1" nor a "?" coding affected the tree topology, and previous analyses with all the miturgids scored "1" resulted also in two independent origins of the precoxal sclerites.

78. Endite shape: variously modified (0); cycloctenid-like (1); zoridlike (2); clubionid-like (3); *Thalassius*-like (4); lycosidlike (5); senoculiid-like (6); *Janusia*-like (7).

Weight = 7.5, L = 8 (2 extra steps), CI = 75, RI = 83

It appears that the endite shape may provide some grouping information at various levels. Throughout the study, a more or less constant pattern was noted among the cycloctenids (as in Forster and Blest, 1979: fig. 40) and *Zora* + Australian relatives. Also, *Clubiona* and *Elaver* share a similar type of endites (strongly concave at the outer basal edge) with *Liocranum*. The endites in *Thalassius* and *Dolomedes* tend to be spoon-shaped, with a smoothly convex outer edge. This condition occurs in *Ancylometes* and it has been used also as an argument for supporting a pisaurid affiliation (Schiappelli and Gerschman de Pikelin, 1970: 156, fig. 19). However, the present data indicate an independent origin in *Ancylometes* as well as in *Hogna frondicola*. This character is scored "?" for *Aglaoctenus*, although it has unmodified endites.

79. Serrula: bordering apex (0); subapical (1); absent (2).

Weight = 4.0, L = 11 (9 extra steps), CI = 18, RI = 70

In all examined taxa, the serrula consists of a single row of strongly to weakly developed teeth,

and nearly bordering the endite apex (fig. 24b, c). This condition is found in amaurobiids, clubionids, and also in *Cupiennius* (Foelix, 1996: fig. 15). The serrula may be smaller and more subapical (fig. 24d, e) as in most examined ctenids. State 2 refers to the condition observed in some of the Australian zorids, which lack a serrula.

80. Labium width: wider than long (0); as wide as long (1); longer than wide (2).

Weight = 2.0, L = 26 (24 extra steps), CI = 7, RI = 53

The labium has played an important role in ctenid taxonomy. A labium wider than long is thought to separate caloctenines from all other ctenids (Keyserling. 1876; Simon, 1897a; Petrunkevitch, 1928; Mello-Leitão, 1940). However, as happens with many other structures, its size and width exhibit a high degree of homoplasy.

81. Labium shape: triangular (0); T-shaped (1); rectangular (2).

Weight = 10, L = 2, CI = 100, RI = 100

A triangular-shaped labium was scored for *Megadictyna*. A T-shaped labium is found in most examined taxa. An almost rectangular labium is found in the senoculids. Although *Peucetia* has also a nearly rectangular labium (Brady, 1964: fig. 139), this taxon was scored "?" since other oxyopids have a T-shaped labium (Brady, 1964: fig. 10). The shape of the labium appears to be diagnostic at the generic level in some of the examined taxa (personal obs.), but in-depth taxonomic revisions are necessary to test this character.

82. T-shaped labium: unmodified (0); *Zora* type (1); *Xenoctenus* type (2); *Vulsor* type (3); *Caloctenus* type (4); *Janusia* type (5); *Cycloctenus* type (6).

Weight = 10, L = 6, CI = 100, RI = 100

83. Labium length: almost as long as endites (0); one-half the endite length (1); less than one-half the endite length (2).

Weight = 5.0, L = 8 (6 extra steps), CI = 25, RI = 82

OCULAR REGION

84. Ocular rows: two (0); three (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 83

85. Ocular pattern: normal (0); lycosid type (1); ctenid type (2); senoculid type (3); *Cycloctenus*-like (4); oxyopid type (5).

Weight = 8.5, L = 6 (1 extra step), CI = 83, RI = 97

Most outgroup taxa have two well-defined ocular rows arranged in what is considered to be a normal pattern (figs. 25a–c, 26a). However, pisaurids (fig. 25e) and zorids (fig. 25g, j) comprise a few genera where the eyes may be arranged in two strongly recurved rows, seemingly forming three lines instead of just two. These taxa have been scored "0" based on the close position of the anterior lateral eyes (ALE) to the anterior median eyes (AME); however, a "1" coding did not affect the final topology.

State 1 refers to a 4–2–2 eye pattern, a condition that is considered synapomorphic for lycosids (Dondale, 1986: 327); the arrangement in *Neoctenus* (fig. 25d) resembles the lycosid pattern, but if it is scored "1" the results indicate that this pattern originated twice; in the final matrix *Neoctenus* was scored "?".

States 2–4 refer to three ocular rows in a 2–4–2 arrangement (figs. 25f, h, i, k, l). This is the so-called ctenid ocular pattern: the AME stand alone in the first row; the ALE lie right underneath the posterior lateral eye (PLE) tubercle, either in a straight or recurved line with the posterior median eyes (PME). The variation observed in this pattern (in congruence with other genitalic and somatic characters) allows, in turn, a partition into three different conditions, each diagnostic at the family level.

State 2 refers to the ctenid pattern sensu stricto. The AME and PME form almost a quadrangle (figs. 25h, l, 26d, 27a, b). This arrangement may vary in some species. For example, *Asthenoctenus* and some species of *Amauropelma* (Raven et al. 2001: fig. 5h) have the ALE removed from the PLE; in the latter, the ocular rows could be very close together, and seemingly the ALE are closer to the AME. The new Australasian genus is a good example of changes involving the ocular region within the Ctenidae. *Amauropelma* comprises species with the typical arrangement (e.g., a new species from Indonesia; Lombok, fig. 26d) as well as others where the eyes are either (1) close together, at first glance forming only two rows (therefore scored "0"); (2) reduced to dark spots; or (3) completely lost. Eyeless species are also known among other ctenid taxa, for example, some undetermined ctenines, some species of *Acantheis*, and *Janusia*. Only the latter was incorporated in the final matrix; all others are known from a single sex and thus their inclusion would add many missing entries. In spite of this, when included, these eyeless species clustered with their respective genera based primarily on genitalic characters. *Janusia* (and the other species, when included) was scored "–" for this character.

State 3 refers to a 2–4–2 arrangement where the median ocular region is almost a rectangle (e.g., fig. 26b), the PLE are sitting at the center

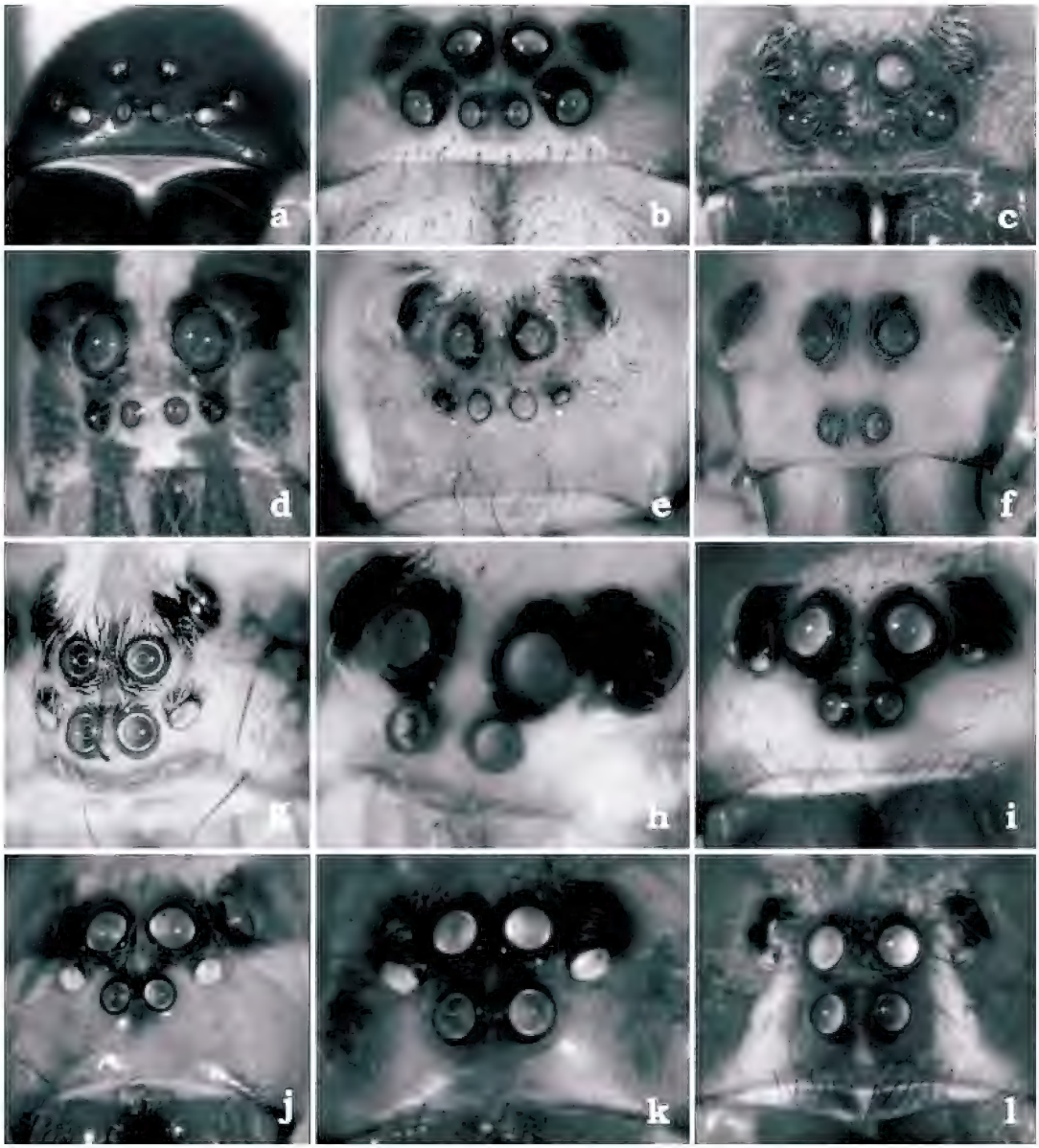

Fig. 25. Female eyes, frontal view. **a.** *Amaurobius ferox* (Walckenaer), showing an entire chilum. **b.** *Griswoldia acaenata* (Griswold). **c.** *Zoropsis rufipes* (Lucas). **d.** *Neoctenus* ca. *comosus* Simon. **e.** *Dolomedes triton* (Walckenaer). **f.** *Senoculus* sp. **g.** *Hestimodema latevittata* Simon. **h.** *Diallomus* ca. *speciosus* Simon. **i.** *Cycloctenus westlandicus* Forster. **j.** *Odo* ca. *lycosoides* (Chamberlin). **k.** *Viracucha andicola* (Simon). **l.** Ctenid, n. sp. (Peru 1), showing a divided chilum.

of an enlarged tubercle, and the ALE are extremely reduced, pearl-shaped, and otherwise unnoticeable. This condition is unique to the senoculids.

State 4 refers to a median ocular region very similar to that in ctenids sensu stricto. However, in all examined species of *Cycloctenus* (apparently the only cycloctenid that has this ocular arrangement), the pattern is almost triangular in shape (e.g., fig. 26c) and the AME are at least two or three times smaller than the PME. A similar condition occurs in a few ctenids (e.g., *Leptoctenus byrrhus*, *Thoriosa*, and *Apolania*). However, all

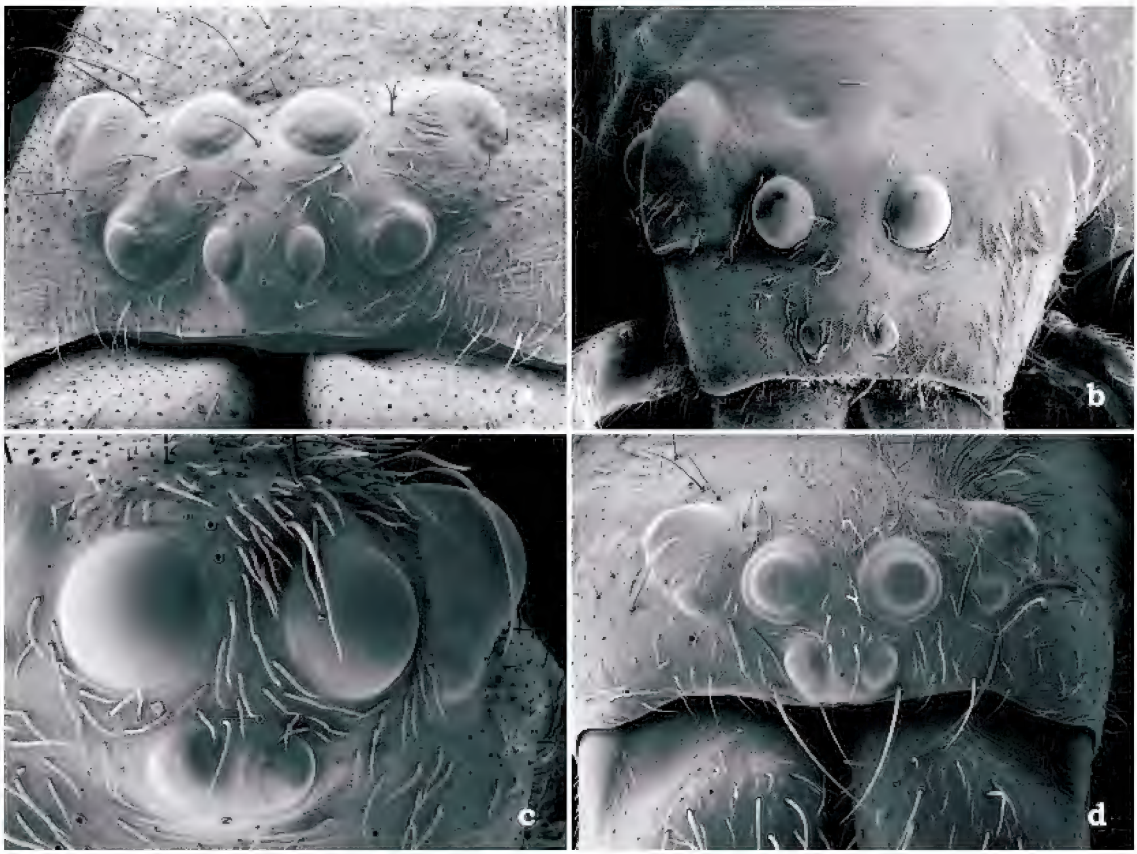

Fig. 26. Female ocular pattern, frontal view. **a.** *Griswoldia acaenata* (Griswold). **b.** *Senoculus* sp. **c.** *Cycloctenus* sp. **d.** *Ctenus miserabilis* Strand.

these ctenid taxa lack numerous unique genitalic and somatic characters of the cycloctenids.

State 5 refers to the hexagonal eye arrangement typical of the Oxyopidae (Brady, 1964: fig. 136).

86. ALE lenses: well developed (0); reduced (1).

Weight = 10, L = 1, CI = 100, RI = 100

The great majority of examined taxa have well-defined, convex ALE lenses (e.g., fig. 25g). By contrast, among *Caloctenus*, *Gephyroctenus*, and all but one species of *Diallomus* the ALE are reduced to flattened structures (e.g., fig. 25h). Because the lenses are not so reduced in a new species of *Diallomus*, this taxon is scored "?".

87. ALE shape: round (0); oval (1); pearl-shaped (2).

Weight = 3.7, L = 12 (10 extra steps), CI = 16, RI = 65

Most outgroups, as well as *Cupiennius*, have the ALE round in shape. State 1 refers to a condition regarded as typical in ctenids. *Ancylometes* and all of the other ctenids have the ALE oval in shape, but this condition occurs also in *Amaurobius ferox* (fig. 25a), *Elassoctenus*, *Argoctenus*, *Strotarchus*, *Eutichurus*, *Tengella*, *Liocranoides*, *Titiotus*, *Zorocrates*, and the Chilean species close to *Phanotea*.

State 2 applies only to *Senoculus* (fig. 25f), which has extremely reduced, pearl-shaped eyes.

88. ALE diameter: one or more times AME (0); as AME (1); about half or less AME (2); larger than AME (3).

Weight = 1.7, L =32 (29 extra steps), CI = 9, RI = 44

In general, the size of the eyes varies greatly across families and also within genera; regardless, it is often used for classification purposes. State 0 refers to ALE about two times larger than the AME and found in such outgroups as *Amaurobius ferox* (fig. 25a), *Phanotea*, *Griswoldia* (fig. 25b), and *Zoropsis* (fig. 25c).

State 1 refers to the ALE as large as the AME; it is scored as present in some species of *Anahita*

Fig. 27. Female tapeta. **a.** *Ctenus* cf. *sinuatipes* F.O.P.-Cambridge (G. Hormiga, photo). **b.** *Viracucha andicola* (Simon), showing posterior median eyes with grate-shaped tapetum.

and in such ctenids as *Ctenus hibernalis* and *C. mitchelli*. State 2 refers to the ALE about half or less the AME diameter, as seen in *Phoneutria* and many other ctenids. State 3 refers to the ALE as large or larger than the AME, though not as large as in state 0; this condition is scored as present in some species of the new Australasian genus and also in *Asthenoctenus*.

89. PME tapetum (char. 28, Griswold et al., 1998): present (0); absent (1).

Weight = 10, L = 1, CI = 100, RI = 100

A tapetum is defined as a reflecting layer appearing either as a narrow line, often along the center of the eyes or forming loops (Homann, 1971) in at least the PME, and is present in a great majority of examined taxa. The reduced tapetum in *Cycloctenus* (Homann, 1968: 52) was scored "0" based on undetermined specimens collected with pyrethrum fogging in northeastern Australia (QMS) and which have the PME with at least three shiny grate-shaped loops.

On the other hand, a tapetum appears to be lacking in *Hestimodema*, *Zora*, *Elassoctenus*, and *Argoctenus*; the latter genus was scored "?" since a shiny grate-shaped tapetum was observed in some undetermined species, presumably members of this taxon.

90. PME tapetum: canoe (0); grate-shaped (1).

Weight = 5.4, L = 6 (5 extra steps), CI = 16, RI = 76

A canoe tapetum, like that observed in *Zorocrates* (Homann, 1971: fig. 27B), is present in *Megadictyna*, the amaurobiids, clubionids, the South American miturgids, *Liocranum*, *Odo* (some species), *Trujillina*, *Uduba*, *Zorodictyna*, and the tengellids.

A grate-shaped tapetum, like that in *Viracucha* (fig. 27b), is present in several examined taxa, for example, *Uliodon*, *Miturga*, an undetermined species from Chile presumably closely related to *Griswoldia*; most ctenids (a few others remain "0", e.g., *Celaetycheus* s.l. and *Apolania*); and *Peucetia* (Kovoor and Muñoz-Cuevas, 1997: 142).

91. PME tapetum crystals: dense, shiny (0); scattered, somewhat opaque (1).

Weight = 6.0, L = 5(4 extra steps), CI = 20, RI = 55

Some of the examined taxa have a grate-shaped tapetum, but it never looks shiny, as in comparable specimens (equal size, sex, degree of preservation) with well-developed tapeta. This condition is attributed to a scarcity of the pigment crystals, but undoubtedly it needs to be studied in more detail; at least in some oxyopids there is a complete lack of reflecting crystals in the tapetum (Kovoor and Muñoz-Cuevas, 1997).

The derived condition is scored for *Peucetia*, *Caloctenus*, and *Gephyroctenus. Diallomus* is still scored "?" because a new species has a shiny tapetum, but of the remaining three known species, at least one has an opaque grate-shaped tapetum. Additional material is required to further examine the tapeta in the other two species.

LEGS

92. Legs: laterigrade (0); prograde (1).

Weight = 10, L = 1, CI = 100, RI = 100

Cycloctenids differ from all other examined taxa in having laterigrade legs (Forster and Blest, 1979: 12). Among other entelegyne spiders, state "0" is characteristic of a few other taxa, being presumably more basal than lycosoids and their kin (see Coddington and Levi, 1991). For example, within the dionychans, laterigrade legs are known among the selenopids and the thomisids. The former have been proposed as close relatives of the cycloctenids primarily based on the structure of the eyes and also on the laterigrade legs (Homann, 1968).

93. Male tibial crack (char. 52, Griswold, 1993: figs. 3, 4): absent (0); present (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 83

The legs break naturally following a peculiar suture line at the base of the male tibiae in *Uduba*, *Raecius*, *Zorodictyna*, *Zoropsis*, *Griswoldia*, *Phanotea*, and the Chilean species. Although *Zorocrates* is thought to be closely related to *Uduba*, it does not have a tibial crack.

94. Trochanter (char. 55, Griswold, 1993: 23): smooth (0); shallowly notched (1); deeply notched (2).

Weight = 4.0, L = 11 (9 extra steps), CI = 18, RI = 25

This character refers to the distal border of the trochanter, which exhibits a range of variation within a single family (Roth, 1964). State 0 refers to an unmodified, fairly smooth trochanter. This condition is scored in *Megadictyna*, the amaurobiids, some cycloctenids, *Liocranum*, and *Clubiona*.

By contrast, all the remaining taxa may have the trochanter shallowly to deeply excavated. State 1 refers to a shallow trochanteral notch, and this condition is observed in cycloctenids (e.g., *C. westlandicus*), as well as in *Elaver*, *Senoculus*, *Psechrus*, and within the ctenids, only in some caloctenine spiders (e.g., Mad 30 and *Gephyroctenus*). State 2 refers to a strongly sclerotized and raised indentation of the trochanter and this is the condition in most of the examined taxa.

95. Pedipalp, ventral tarsus: unmodified (0); stiff setae (1); clavate setae (2); two short macrosetae (3); spiny (4); brushlike (5); *Xenoctenus* type (6).

Weight = 5.0, L = 12 (6 extra steps), CI = 50, RI = 75

State 0 refers to a palpal tarsus covered with normal hairs, as occurs in *Megadictyna* and most of the examined taxa. State 1 refers to a type of ventral, stiff macrosetae found among the Malagasy ctenids (e.g., fig. 28c). State 2 refers to strong, clavate setae, present in *Zora* and closely related taxa. State 3 refers to two strong macrosetae lying near the apex of the tarsus (e.g., fig. 28d), as in *Thoriosa* and *Amauropelma*. State 4 refers to ventral spines (e.g., fig. 28a), such as those among the amaurobiids, cycloctenids, and senoculids. Although *Liocranum* has been scored "4", its condition may indeed correspond to a new state. State 5 refers to a dense brush of setae scored in *Eutichurus* and *Miturga*. This brush is absent in *Strotarchus* and is still uncertain for *Teminius*. State 6 refers to the combination of modified apical setae and short macrosetae (e.g., fig. 28b) found in *Odo* ca. *lycosoides* and closely related species.

96. Femur I, dorsal spines: none or 1 (0); 0–1–1 (1); 1–1–1 (2).

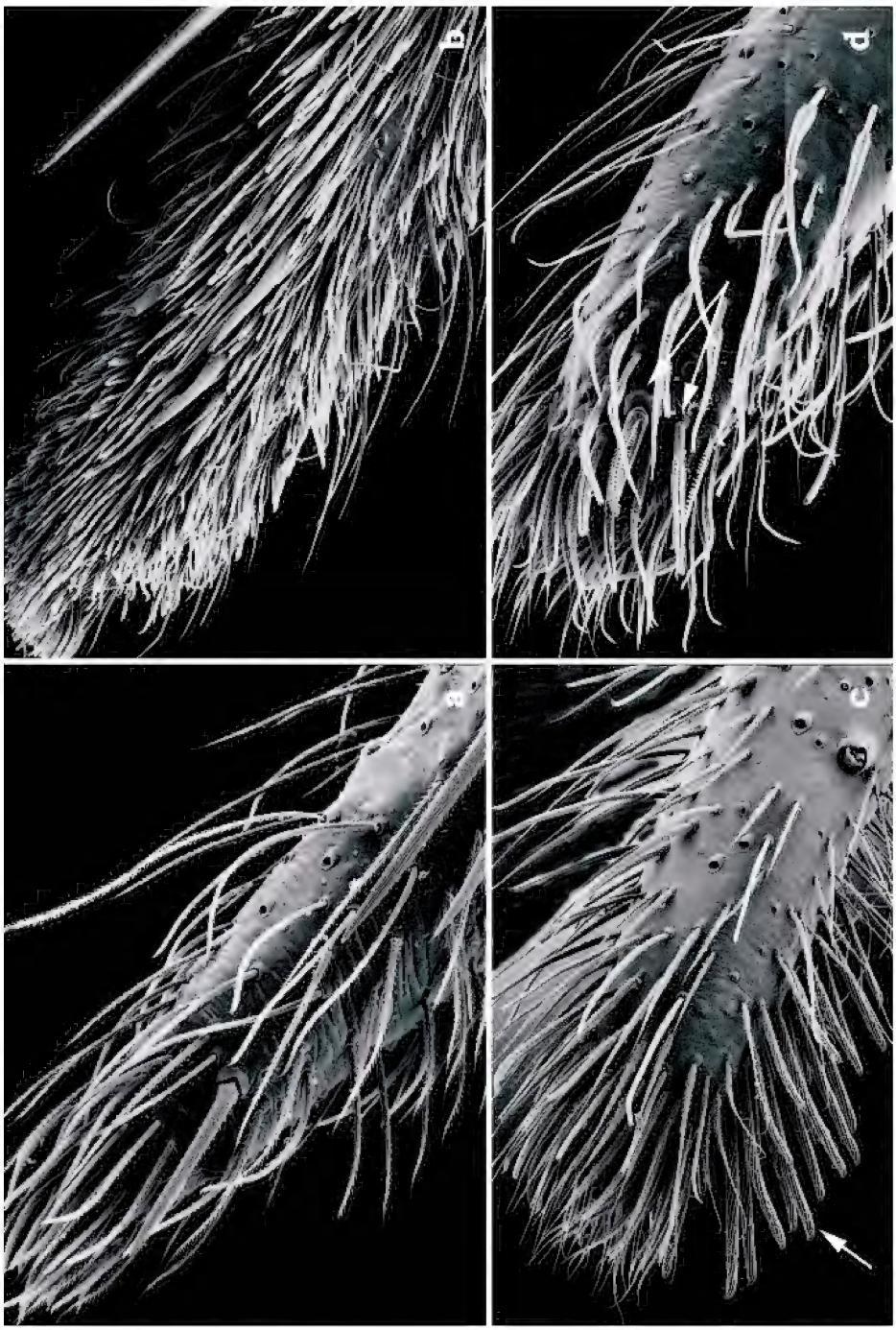

Fig. 28. Female pedipalp, ventral view. **a.** *Amaurobius ferox* (Walckenaer). **b.** *Odo* ca. *lycosoides* (Chamberlin). **c.** Viridasine, Madagascar 25, arrow points to modified setae. **e.** Ctenid, n. sp. (Lombok), arrows point to two enlarged setae.

Weight = 4.6, L = 9 (7 extra steps), CI = 22, RI = 36

Across taxa, the femoral spination pattern tends to be constant on all the legs; however, among a few taxa, only the anterior legs may have greatly reduced spination. Therefore, character 96 refers only to the number of dorsal spines on the femora of the first pair of legs. State 0 is scored in *Megadictyna*, *Pimus*, *Uduba*, *Raecius*, and *Zorodictyna*. State 1 refers to the occurrence of two dorsal spines, and it is scored as present in *Amaurobius ferox*, *Liocranum*, *Strotarchus*, *Eutichurus*, *Uliodon*, *Psechrus*, and Mad 30. State 2 refers to femora with three dorsal spines; this is the condition in the great majority of examined taxa.

97. Tibia I, ventral spines (char. 59, Griswold, 1993: 23): 2–2–2 (0); 2-2-2-2 (1); 2-2-2-2-2 (2); 2-2-2-1-2 (3); 6 to 10 (4); 2–2–0 (5); 1–2–0 (6); 10 or more (7); 5 + 1 (8).

Weight = 2.0, L = 31 (23 extra steps), CI = 25, RI = 54

In general, the leg spination exhibits a great deal of variation at the family level. State 0 refers to three pairs of ventral-paired spines beneath tibiae I (e.g., *Megadictyna*, the amaurobiids, and most viridasine spiders). State 1 (only four ventral-paired spines) is scored in some species of *Cycloctenus*, *Tengella*, *Dolomedes*, *Thalassius*, *Ancylometes*, and *Cupiennius*. State 2 (five ventral-paired spines) is the most common in all examined taxa, including the great majority of ctenids. State 3 is regarded as an autapomorphy of *Griswoldia* (Griswold, 1991), and in this matrix it is scored as present also in *Zorocrates*. State 4 refers to the occurrence of 6–10 pairs of ventral spines; it is scored in *Liocranum*, such tengellids as *Titiotus* and *Liocranoides*, as well as in *Zora*, *Elassoctenus*, *Trujillina*, *Zoropsis*, and some ctenids (e.g, acanthoctenines and acantheines). State 5 (only two pairs of ventral spines) is scored in the clubionids. State 6 refers to the spination in *Eutichurus*, a single middle pair plus one distal spine. State 7 refers to 10 or more pairs of ventral spines beneath tibia I; this condition is observed in some species of *Senoculus* (others have only five pairs), some species of *Acantheis*, and also in *Gephyroctenus*.

98. Metatarsus I, ventral spines: 2–2–2 (0); 2-2-2-2 (1); 2–2–0 (2); 2-2-2-2-2 (3); 2-2-2-1 (4); 2–0–0 (5); 6 to 12 pairs (6); 2–2–1 (7).

Weight = 2.3, L = 27 (20 extra steps), CI = 25, RI = 54

As in the above character, metatarsal spines vary greatly across taxa. Although a great majority of ctenids have three pairs, some others (e.g., *Vulsor* and *Viridasius*) have only one pair, as occurs in the two clubionids examined, some zorids, and also the miturgids. In contrast, other ctenids (e.g., Mad 2) have two pairs of ventral spines, resembling the condition in such zorids as *Hestimodema* or *Elassoctenus*. The presence of 6–12 metatarsal pairs of spines appears to be synapomorphic for *Caloctenus* and *Gephyroctenus*, and is independently derived in some species of *Senoculus*. *Strotarchus*, *Eutichurus*, and *Neoctenus* have only two pairs of ventral spines plus a single one beneath metatarsi I.

99. Tibia I, ventral spines: no overlap (0); slight overlap (1); strong overlap (2).

Weight = 2.4, L = 21 (19 extra steps), CI = 9, RI = 56

In most examined taxa, the ventral spines beneath tibiae I are rather short and well separated, whereas in some others (e.g., *Ctenus hibernalis*) there is an overlap between one or two pairs of spines. State 2 refers to fairly long overlapping spines as occurs in the liocranids and some ctenids (e.g., *Acanthoctenus*, *Acantheis*, *Caloctenus*, *Gephyroctenus*, and *Enoploctenus*).

100. Tibia I, distal paired ventral spines: absent (0); present (1).

Weight = 4.0, L = 10 (9 extra steps), CI = 10, RI = 67

The absence of the most distal pair of tibial spines is considered one of the characters supporting a close relationship between *Petaloctenus* and *Africactenus* and therefore the affiliation of the former genus to the acantheines (Jocqué and Steyn, 1997: 116). In the present matrix, this character appears to be plesiomorphic; it occurs in *Megadictyna*, *Pimus* (however, it is present in *Amaurobius*), in two of the three cycloctenid species, the clubionids, and a few other outgroups. Within ctenids, it is absent in the acanthoctenines, caloctenines, *Africactenus* (present in *Acantheis* and *Enoploctenus*), and a few others (e.g., some species of *Anahita*).

101. Preening comb: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Preening combs, distalmost straight macrosetae arranged either in a row or like a brush on the metatarsi of some taxa (Ovshtarenko, personal commun.), were found on legs III and IV in both *Strotarchus* and *Eutichurus*.

102. Calamistrum: present (0); absent (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 75

This structure is made of modified setae that handle the silk coming from the cribellum. The occurrence of a calamistrum and a cribellum is generally thought to form part of the groundplan of several spider families (Griswold et al., 1999; Platnick, 1977).

103. Calamistrum: linear (0); oval (1).

Weight = 10, L = 1, CI = 100, RI = 100

A calamistrum formed by hairs of about the same length and extending in a narrow line, almost as long as the metatarsi, appears to be the plesiomorphic condition among cribellates (char. 14, Griswold et al., 1999); state 0 was scored in *Megadictyna* and the amaurobiids. In the derived condition, the calamistrum hairs have a variable length and often form at least five short irregular rows roughly in a proximal position. This condition was scored in all of the remaining cribellates.

104. Tarsal scopula: absent (0); present (1).

Weight = 3.3, L = 13 (12 extra steps), CI = 7, RI = 40

Dense scopulae, that is, hairs with modified tips for better prey-gripping or adhesion to smooth surfaces (Foelix, 1996: 18), are perhaps one of the most typical structures associated with ctenids as well as many other hunting spiders. A tarsal scopulae is lacking in *Megadictyna*, the amaurobiids, the cycloctenids, some other outgroups, and some ctenids (e.g., fig. 29f).

105. Tarsal scopula: light (0); dense (1).

Weight = 4.2, L = 9 (8 extra steps), CI = 11, RI = 38

Among the examined taxa, in particular within the ctenids, there is a great range of variation involving the density of the tarsal scopulate hairs (e.g., fig. 29a–f).

Across the examined taxa, state 0 (tarsal scopula with sparse hairs) is scored in *Aglaoctenus*, some zorids (e.g., *Zora spinimana*), and such ctenids as *Celaetycheus* ca. *flavostriatus*, *Janusia*, some species of *Acantheis*, and a few others. State 1 (a well-developed tarsal scopula) is characteristic of various taxa, for example, clubionids (fig. 31a), *Zoropsis* (fig. 29c), miturgids (fig. 29d) some zorids, and several ctenids (e.g., fig. 29e).

106. Claw tufts: absent (0); present (1).

Weight = 3.7, L = 11 (10 extra steps), CI = 9, RI = 66

Among the examined taxa, the claw tufts are mostly formed by lamelliform setae (Platnick and Lau, 1975). However, the hair density and the kind of lamellate setae tend to be rather variable (e.g., fig. 29a—f), but this variation is still hard to quantify; therefore, only the presence of claw tufts was considered in this analysis. Although some taxa (e.g., *Neoctenus*, *Psechrus*, and *Griswoldia*) apparently have dense claw tufts, they were scored "0" because they are not claw tufts in the strict sense. In these cases (e.g., fig. 29b), the tarsal scopula extends underneath the claws, and hairs are not lamelliform but are spikelike (Platnick and Lau, 1975).

107. Claw tufts: light (0); dense (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 62

Among the examined taxa, some have a light claw tuft, sometimes even reduced to just four or five tenant hairs (state 0) (e.g., fig. 29f). The condition in most ctenid taxa and some outgroups is the occurrence of densely compact pads of claw tufts (state 1) (e.g., fig. 29e).

108. Metatarsal trichobothria: none or one (0); one row (1); two or three rows (2).

Weight = 5.4, L = 7 (5), CI = 28, RI = 64

Megadictyna has a single trichobothrium on metatarsi I–III and none on metatarsus IV (Harvey, 1995: 281). A single row of trichobothria was scored in the amaurobiids and cycloctenids. All the remaining taxa have at least two trichobothrial rows.

109. Tarsal trichobothria: none or one (0); one row (1); two or three rows (2).

Weight = 8.5, L = 3 (1 extra step), CI = 66, RI = 80

In *Megadictyna* there is a single tarsal trichobothrium, whereas in the remaining taxa the trichobothria may be distributed in a single row, as in the amaurobiids, or in two or more rows, as in the ctenids. In almost all of the examined taxa, the trichobothria increase in length from proximal to distal, with the most distal trichobothrium located either close to the claws or more toward the middle of the segment.

110. Tarsal claws: three (0); two (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 80

Three tarsal claws are regarded as the plesiomorphic condition for spiders (Platnick, 1999: 2; Coddington and Levi, 1991: 583). A great majority of the examined taxa, including most ctenids, have only two tarsal claws, at least as adults.

111. Inferior tarsal claw (ITC): large (0); small (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 76

When present, the ITC appears to be rather variable. The ITC is large and well developed in *Cycloctenus* and *Senoculus*, but is small, sometimes reduced to a nubbin, in some others, even in some taxa with well developed claw tufts (e.g., *Anachemmis* and *Cupiennius*). Also, such genera as *Griswoldia*, *Phanotea* (Griswold, 1991, 1994), and *Janusia* may have a small ITC on the anterior legs and only nubbins or none on the posterior legs.

112. Inferior tarsal claw: toothed (0); smooth (1).

Weight = 7.5, L = 3 (2 extra steps), CI = 33, RI = 66

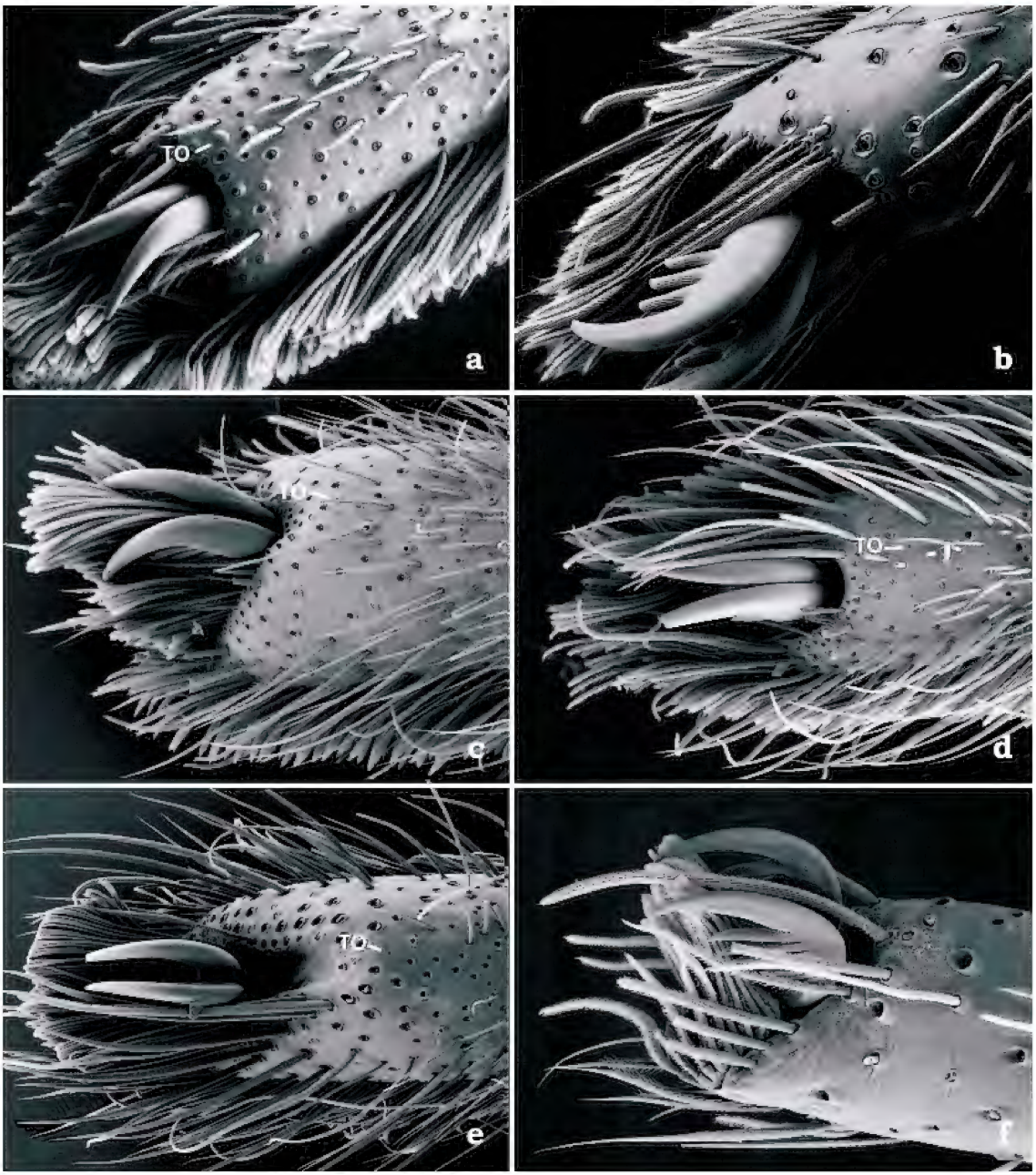

Fig. 29. Claw tufts and scopula, female left tarsus I. **a.** *Elaver texana* (Gertsch). **b.** *Griswoldia acaenata* (Griswold). **c.** *Zoropsis rufipes* (Lucas). **d.** *Miturga lineata* Thorell. **e.** *Viracucha andicola* (Simon). **f.** *Gephyroctenus* cf. *philodromoides* M.-Leitão. Arrows show position of tarsal organ.

The presence and number of tarsal claw teeth are also rather variable. Although cycloctenids are described as having an ITC with small teeth, some of the species examined have a rather smooth ITC. All the remaining three-clawed spiders have a smooth ITC. It appears that this variation arises very early in the development of the spiders. For instance, some ctenid nymphs may have ITC teeth (Homann, 1971: 264); however, they are lacking in eyeless nymphs of *O. medius* (by contrast, nymphs of *Cupiennius salei* have an ITC with a single tooth, which is lost in later stages).

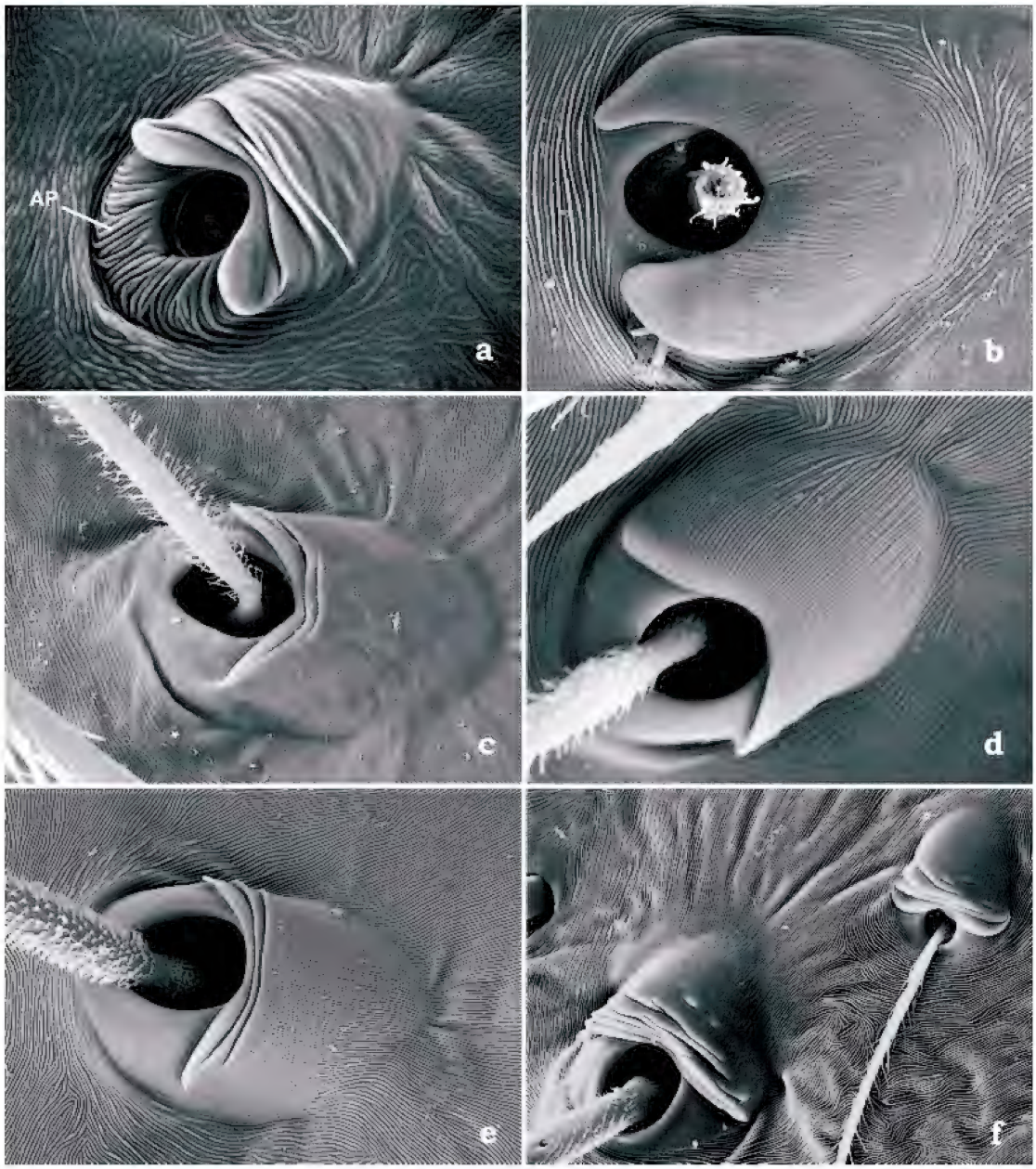

Fig. 30. Trichobothria, female left tarsus I. **a.** *Amaurobius ferox* (Walckenaer), AP = apical plate. **b.** *Cycloctenus* ca. *flaviceps* Koch. **c.** *Viridasius fasciatus* (Lenz). **d.** *Vulsor isaloensis* (Ono). **e.** *Viracucha andicola* (Simon). **f.** *Ctenus mitchelli* Gertsch.

113. Trichobothrial hood: normal (0); projecting laterally (1).

Weight = 10, L = 1, CI = 100, RI = 100

In cycloctenids the trichobothrial dorsal plate or hood is projecting laterally (e.g., fig. 30b; see also Forster and Blest, 1979: figs. 1–4).

114. Trichobothria hood ridges: none (0); less than 3 (1); 3 or more (2).

Weight = 2.8, L = 17 (15 extra steps), CI = 11, RI = 48

A smooth trichobothrial hood (i.e., without transverse ridges; e.g., fig. 30b, d) is observed in

such taxa as *Megadictyna*, *Cycloctenus*, *Senoculus*, *Lycosa*, some zorids, and some ctenids. By contrast, others (e.g., some other zorids and ctenids) may have one large transverse ridge with or without smaller lines (fig. 30c, e). The great majority of examined taxa have more than three large transverse ridges (fig. 30f).

115. Trichobothria apical plate: smooth (0); rugged (1).

Weight = 10, L = 1, CI = 100, RI = 100

The trichobothrial apical plate (e.g., one directed toward the claws) has a series of parallel, strong ridges (fig. 30a) in both *Pimus napa* and *Amaurobius ferox*. This character may prove useful for elucidating phylogenetic relationships among amaurobiid spiders.

116. Tarsi: straight (0); slightly bent (1); strongly curved (2).

Weight = 8.5, L = 3 (1 extra step), CI = 66, RI = 83

Cycloctenids and senoculids have the tarsi slightly bent. Strongly curved tarsi (= the flexible tarsi in Carico, 1993: 229, 237) appear to be common in some trechaleids (e.g., *Trechalea*, *Syntrechalea*, and *Hesydrus*).

117. V-shaped tarsal aperture: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

In dorsal view, the tarsi in the great majority of taxa are smoothly rounded near the claws (e.g., fig. 29a) or slightly indented (e.g., fig. 29c). The derived condition refers to a rather large V-shaped indentation (e.g., fig. 29e) observed in *Acanthoctenus*, *Nothroctenus*, and *Viracucha*.

118. Female palpal tarsus: conical (0); truncated (1).

Weight = 10, L = 1, CI = 100, RI = 100

Females of both *Clubiona* and *Elaver* have the palpal tarsus truncated. In a recent revision of eutichurines (Bonaldo, 1994: 104), a truncated female palp is considered diagnostic for the subfamily. My examination of *E. radulphius* showed certain resemblance to that found in clubionids, and so it was also scored for state 1; however, *Strotarchus* was scored "?" even though it appears to have a normal female palp. In the remaining miturgids, as well as all other examined taxa, the female palp is more or less conical.

ABDOMEN

119. Abdominal modified setae: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 66

In general, dorsal modified setae (often covering the entire body) appear to be independently derived in various spider families. Unfortunately, it is still very hard to establish accurate homologies among the various types of modified setae examined in some taxa. For this reason, only a few of them were considered for this analysis. In addition to scalelike setae, some taxa may have laterally compressed setae that resemble scales with an elongated pedicel. This kind of setae appears to be an autapomorphy for a new genus of Malagasy ctenids (e.g., Mad 2), which also has the entire body covered by bright-colored green and red-orange club-shaped setae.

120. Abdominal dorsum, leaf-shaped setae: absent (0); present (1).

Weight = 10, L = 1, CI = 100, RI = 100

Scales or leaflike setae are used for taxonomic purposes at various levels within the Salticidae (Hill, 1979; Galiano, 1975). However, the same kind of scales (in terms of position and structure) are known in oxyopids and gnaphosids (Townsend and Felgenhauer, 1998), lycosids (Alderweireldt, 1992), as well as in selenopids and ctenids (personal obs.). Leaf-shaped setae were scored for a new caloctenine genus from Madagascar (Mad 30), *Gephyroctenus*, and *Caloctenus*. The former two have a bright green coloration, while the latter exhibits a brownish gray pattern with bright orange leaf-shaped setae.

121. Abdominal dorsum, club-shaped setae: absent (0); present (1).

Weight = 6.6, L = 4 (3 extra steps), CI = 25, RI = 25

A kind of club-shaped, red-orange setae appears to be common in *Gephyroctenus*, *Acantheis*, and some species of *Enoploctenus*; scattered hairs of this type are also found in some species of *Africactenus*. Club-shaped setae were scored also for a new genus of viridasines (Mad 2).

122. Heart ostia: three pairs (0); two pairs (1).

Weight = 10, L = 1, CI = 100, RI = 100

Among the examined taxa, only *Senoculus* has two pairs of heart ostia (Petrunkevitch, 1933: 349, fig. 33).

123. Median tracheae: strongly branched (0); slightly branched (1); unbranched (2).

Weight = 8.5, L = 3 (1 extra step), CI = 66, RI = 50 A hypothesis based on tracheal structure separates the araneomorph spiders into two main groupings, Amaurobioidea and Dictynoidea (Forster, 1970: 12). Amaurobioids are characterized by slender unbranched tracheal tubes, while dictynoids should have at least the median tracheae strongly branched.

The great majority of taxa examined in this

study should belong to Forster's amaurobioids, since they have four unbranched tracheal tubes. However, the range of variation in several other morphological characters across taxa does not allow a clearcut recognition of suprageneric lineages in the way this hypothesis indicates. Further, the tracheal tubes have different origins—the lateral tubes are homologous with the second pair of booklungs, while the median tubes are homologous with a pair of apodemes to which the ventral longitudinal muscles of the third abdominal segment are attached (Ramirez, 2000; Forster, 1970: 14; Purcell, 1909: 60, 76, fig. 31).

The median tracheae are strongly ramified in *Megadictyna*, slightly branched in *Zora* (Lamy, 1902: 211, fig. 55), *Hestimodema* nr. *latevittata*, and *Argoctenus* sp., but are not unknown among lycosids, for example, in *Hogna frondicola* (personal obs.) and *Lycosa nemoralis* (see Lamy, 1902: 220, fig. 65). All the remaining taxa have slender unmodified median tracheae.

124. Lateral tracheae: none (0); two, unbranched (1); two, branched (2).

Weight = 7.5, L = 4 (2 extra steps), CI = 50, RI = 33

Lateral tracheae are lacking in *Megadictyna*, *Ctenus amanensis*, *Anahita punctulata*, and a new species of *Anahita* from New Caledonia. Most examined taxa have two unbranched lateral tracheae. By contrast, the lateral tracheae in *Miturga lineata* bifurcates near the base into two slender tubes, with the inner branch being roughly half the size of the outer branch (personal obs.).

125. Epiandrous gland spigots (char. 56, Griswold et al., 1999): present (0); absent (1).

Weight = 5.0, L = 7 (6 extra steps), CI = 14, RI = 76

The presence of modified setae connected to the epiandrous glands in males of several unrelated families is a plesiomorphic condition; however, their arrangement may show a broad range of variation within a single family, for example, in the tetragnathids, salticids (Lopez and Emerit, 1988: figs. 1, 13–16), and oxyopids (Kovoor and Muñoz-Cuevas, 1998: 138, 140, fig. 1). Although this kind of variation may prove useful for elucidating phylogenetic relationships at infrageneric levels, it is still very hard to score accurately.

Epiandrous gland spigots (fig. 31a–f) are scored for such taxa as *Megadictyna* (Griswold et al., 1999), amaurobiids, zorids, and viridasines. There are a few genera that have not been examined for this character (e.g., *Liocranum*); however, based on the examination of *Agroeca pratensis*, this taxon was scored "0", though it may lack epiandric spigots after all. By contrast, most examined taxa lack epiandrous spigots; for example, most cribellate spiders (e.g., *Psechrus*, *Zoropsis*, and the acanthoctenines), as well as all examined ecribellates (e.g., *Aglaoctenus*, *Zorocrates*, *Titiotus*, *Anachemmis*, and several ctenids).

126. Anal tubercle: rounded (0); pointed (1); prominent cone (2).

Weight = 10, L = 2, CI = 100, RI = 100

The great majority of examined taxa have a more or less rounded and relatively small tubercle; the clubionids are characterized by having the anal tubercle projected into an acute cone, whereas senoculids have a fairly large and obtuse tubercle.

127. Anal setae: normal (0); thick (1).

Weight = 10, L = 1, CI = 100, RI = 100

Among the examined taxa, only the caloctenines (e.g., *Gephyroctenus* and *Diallomus*) have elongate and thick setae bordering the anal region ventrally (Silva, 2001).

128. Female colulus: two hairy plates (0); hairy (1); short lobe (2); reduced or absent (3).

Weight = 2.1, L = 25 (22 extra steps), CI = 12, RI = 45

The colulus exhibits a high degree of homoplasy across all examined taxa. In this study, both males and females of *Clubiona* and *Elaver* have a paired, hairy colulus, which appears to be a general condition among the clubionids (Kovoor, 1977: 132). Although the colulus in *Senoculus* appears as a single-haired structure under the stereoscope, SEM examination shows a bipartite condition in at least one species. A single, hairy colulus is observed in *Liocranum*, miturgids, some zorids, lycosids, and the Malagasy ctenids. A short lobe occurs in various taxa (e.g., cycloctenids, tengellids, pisaurids, and some ctenids). The colulus is reduced or completely lost in some zorids and ctenids (e.g., *Anahita*).

SPINNERETS

129. Cribellum: entire (0); divided (1); absent (2)

Weight = 5.4, L = 7 (5 extra steps), CI = 28, RI = 54

The presence of a cribellum is considered a synapomorphy for all Araneomorphae (Platnick, 1977: 7); however, the loss of a cribellum has occurred several times (Griswold et al., 1998: 40). An entire cribellum (fig. 32e) is characteristic of *Megadictyna*, *Viracucha*, and some species of *Nothroctenus*. Even though *Raecius* seemingly has a divided cribellum (fig. 32c), under the stereomicroscope this structure looks entire and therefore was scored "0". All the remaining cribellates have a divided cribellum,for example, *Amaurobius* (Foelix, 1996: fig. 103), *Zoropsis*

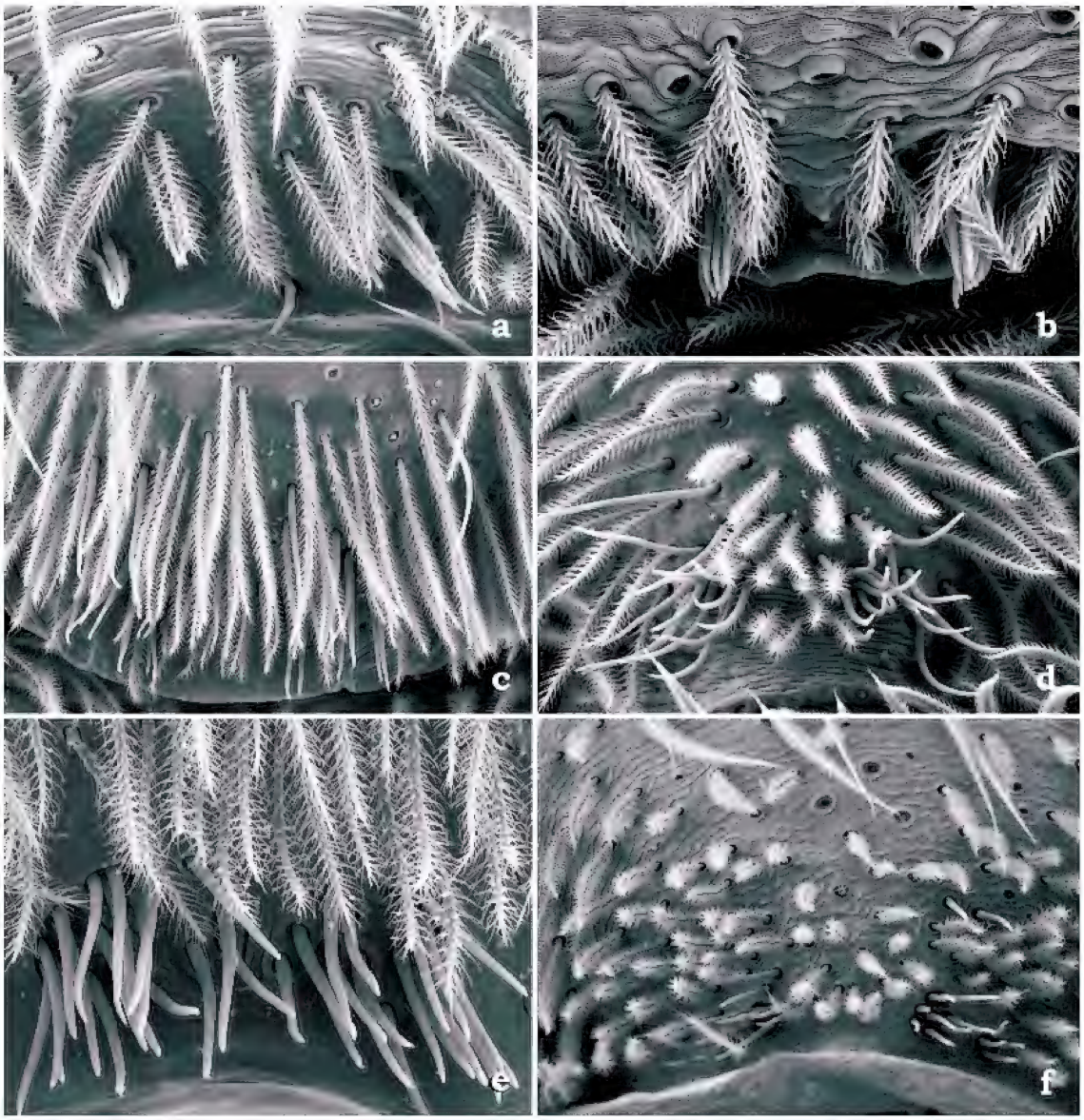

Fig. 31. Male abdomen, ventral view showing epiandrous gland spigots. **a.** *Odo* sp. (Chile). **b.** *Zora spinimana* (Sundevall). **c.** *Miturga lineata* Thorell. **d.** *Uliodon tarantulinus* (L. Koch). **e.** *Viridasius*, n. sp. (Mad 7). **f.** *Vulsor*, n. sp. (Mad 11).

(fig. 32a), and *Acanthoctenus*. The cribellum is lost in the great majority of examined taxa.

130. Cribellate spigots (char. 61, Griswold et al., 1999): dispersed (0); in clusters (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 50

It appears that the ancestral condition for cribellate spiders is the occurrence of single spigots uniformly distributed (e.g., fig. 32b, f). The derived state refers to cribellate spigots arranged in clusters, as occurs in *Raecius* (fig. 32c), *Uduba*, and *Acanthoctenus*.

131. Posterior lateral spinneret distal segment: short (0); elongated (1).

Weight = 8.5, L = 2 (1 extra step), CI = 50, RI = 66

A short posterior lateral spinneret (e.g., fig. 33a) is observed in a great majority of examined

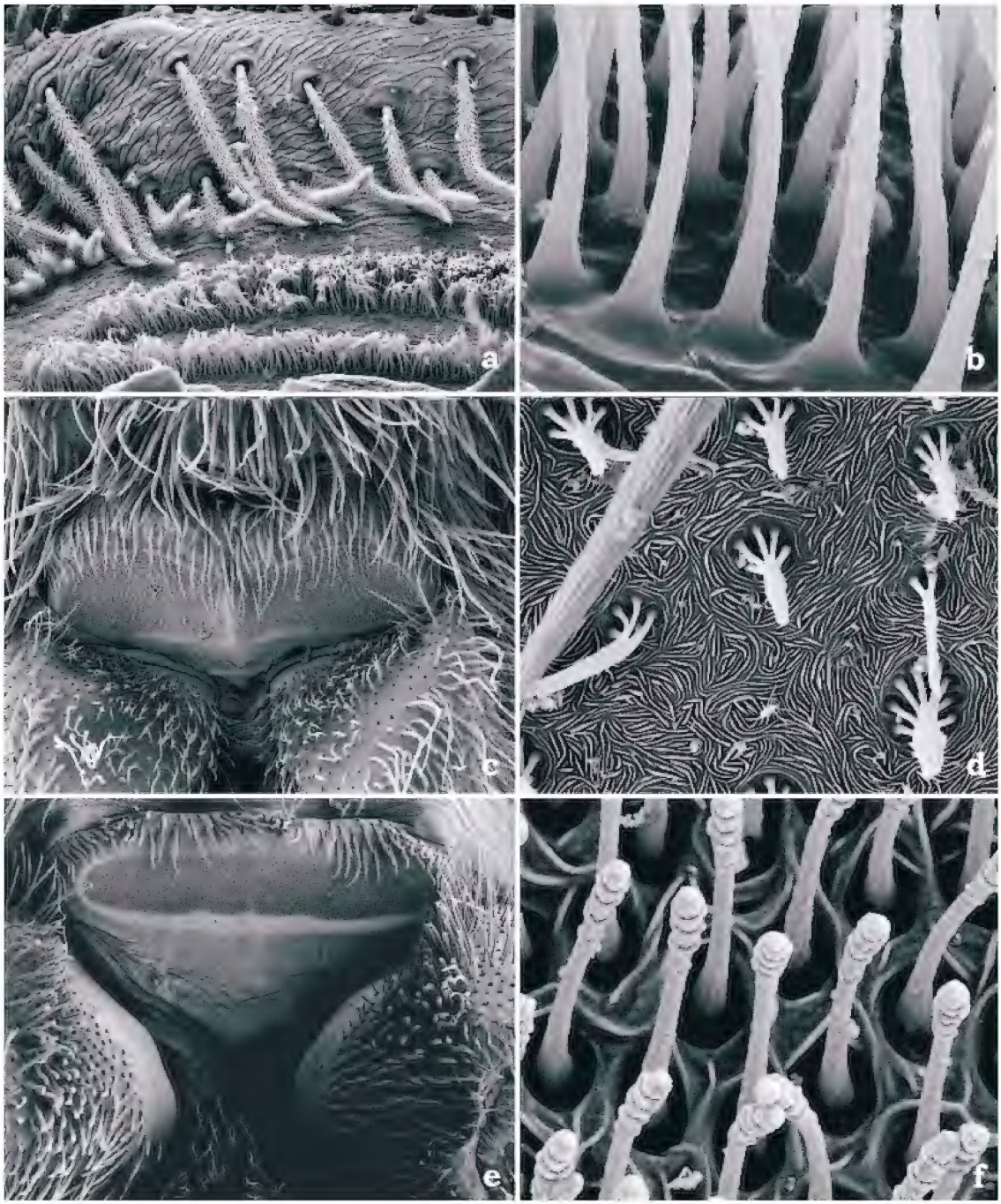

Fig. 32. Female abdomen, ventral view showing cribellum. **a, b.** *Zoropsis rufipes* (Lucas), left side of cribellum and closeup of spigots. **c, d.** *Raecius* sp. **e, f.** *Viracucha andicola* (Simon.).

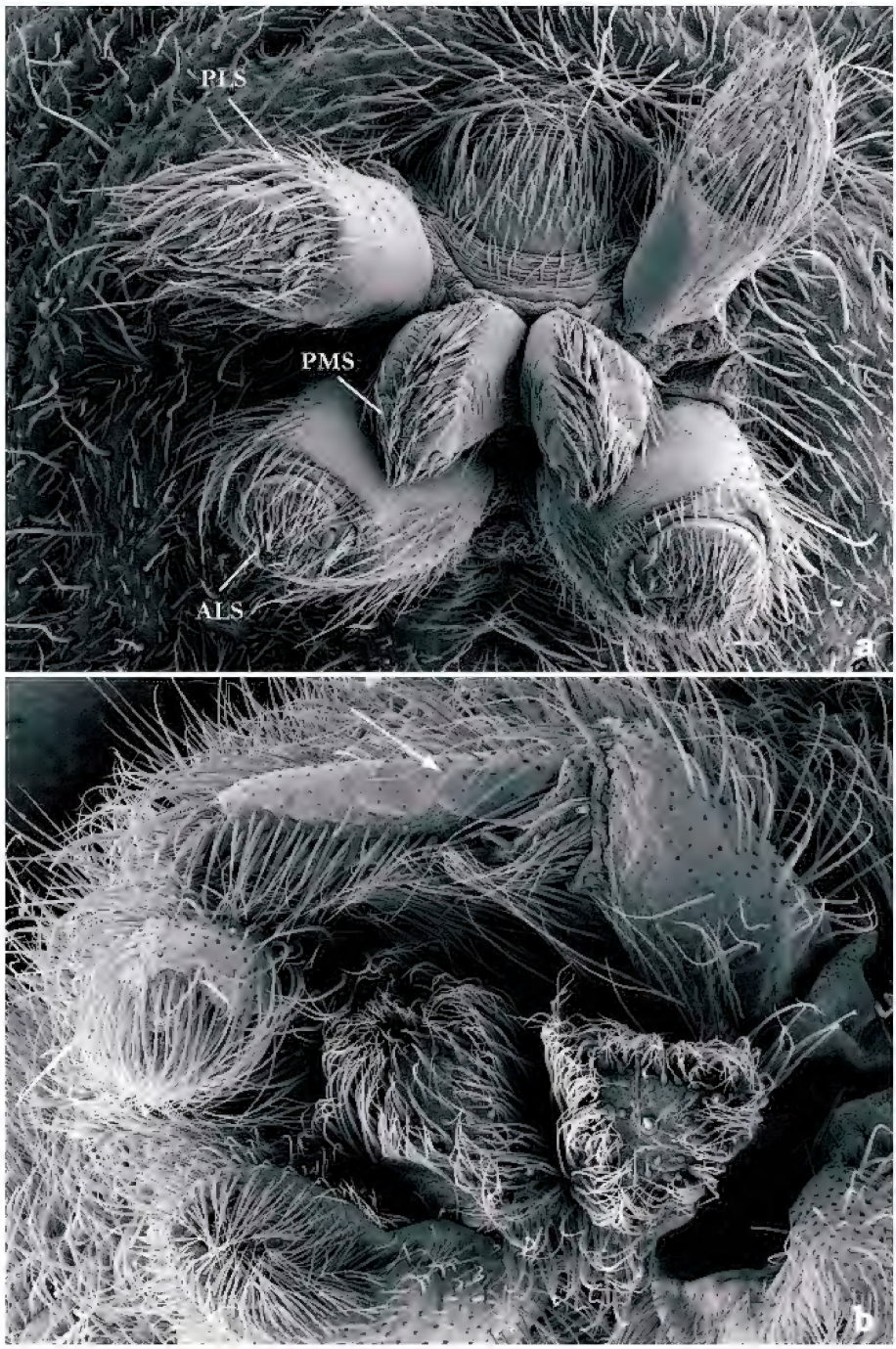

Fig. 33. Female spinnerets. **a.** *Anachemmis sober* Chamberlin. **b.** *Miturga lineata* Thorell, arrow points to enlarged PLS basal segment. ALS = anterior lateral spinneret, PLS = posterior lateral spinneret, PMS = posterior median spinneret

taxa. Among miturgids, eutichurines and miturgines are recognized by having the posterior lateral spinnerets with the distal segment greatly elongated and often more slender than the basal segment (Ramirez et al., 1997: 45; Platnick and Shadab, 1989: 2). In this study, *Eutichurus*, *Strotarchus*, *Miturga*, and *Teminius* clearly show an enlarged distal segment (e.g., fig. 33b); however, it is not so well differentiated in *Uliodon*.

132. Spigot cuticle: concentric ridges (0); longitudinal ridges (1).

Weight = 10, L = 1, CI = 100, RI = 100

In amaurobiids and some cycloctenids, the spigot cuticle has a series of concentric ridges. Although it was not examined in *Megadictyna*, which remains unknown, concentric ridges were observed in *Titanoeca*, which is the next most basal taxon after the nicodamids (Griswold et al., 1999). By contrast, all the remaining taxa have spigots with longitudinal ridges.

133. Piriform spigots: more than 10 (0); 10 or fewer (1).

Weight = 6.0, L = 5 (4 extra steps), CI = 20, RI = 42

A reduction in the number of piriform spigots was observed in *Zora*, *Hestimodema*, *Argoctenus*, *Elassoctenus*, *Diallomus*, *Gephyroctenus*, and at least two new undescribed species from Bali and Australia.

Many of the examined taxa have more than 10 piriform gland spigots; however, there are a few for which this character is still unknown, which is the case for various South American zorids, *Apolania*, and *Celaetycheus*.

134. Male piriform spigots: rounded (0); enlarged (1).

Weight = 10, L = 1, CI = 100, RI = 100

Clubionids are one of the very few spider families where the males have the anterior lateral spinnerets with greatly enlarged piriform gland spigots (Ramirez et al., 1997: 44, fig. 26, 29; Platnick and Di Franco, 1992: 5, fig. 4; Platnick, 1990: 35); enlarged piriforms were observed in *Clubiona* and *Elaver*. All other remaining taxa have normal spigots.

135. Paracribellar spigots (char. 77, Griswold et al., 1999): present (0); absent (1).

Weight = 10, L = 1, CI = 100, RI = 100

Paracribellar spigots (fig. 34a) are reported in *Megadictyna* (Griswold et al., 1999). Such spigots, recognized by their spiral-like or annulated shafts (Coddington, 1989: 76), were observed in the posterior median spinnerets of the two amaurobiids and also in *Titanoeca americana*, the next most basal taxon after *Megadictyna* (Griswold et al., 1999). All the remaining cribellate spiders, including the three cribellate ctenid genera, lack this kind of spigot.

136. Minor ampullate female spigots: one (0); two (1).

Weight = 4.0, L = 10 (9 extra steps), CI = 10, RI = 30

The great majority of examined taxa have two minor ampullates (e.g., fig. 34c); by contrast, only one minor ampullate gland spigot was scored in *Megadictyna*, *Psechrus*, *Tengella* (Griswold et al., 1999), *Liocranoides* (Platnick, 1999), and, within ctenids, in at least one new species from Indonesia (Lombok).

137. Minor ampullate spigots: on mound (0); separated by their diameter (1); close together (2).

Weight = 4.6, L = 9 (7 extra steps), CI = 22, RI = 50

State 0 refers to a minor ampullate gland spigot plus a nubbin arising from an enlarged cuticular projection (e.g., fig. 34c, d), as occurs in *A. ferox*, *Odo insularis*, *Griswoldia* (Griswold, 1991: fig. 35), *Miturga*, *Uliodon*, and the Malagasy ctenids, among a few others. More often the two minor ampullates are side by side on the anterior margin of the posterior median spinnerets (e.g., fig. 34b), but in a few other groups they are separated by at least their diameter (e.g., fig. 34c).

138. Posterior median spinnerets, cylindrical spigots: present (0); absent (1).

Weight = 10, L = 1, CI = 100, RI = 100

Cylindrical gland spigots are present in most of the examined taxa, including *Uliodon tarantulinus*, *Miturga lineata* (fig. 34c), and *Teminius affinis*. On the other hand, the absence of cylindrical glands has been reported in clubionids and a few other unrelated taxa (Kovoor, 1977: 143). The loss of cylindrical spigots has been reported also in some miturgids, for example in *Strotarchus* and *Eutichurus* (Ramirez et al., 1997: 44).

139. Posterior median spinnerets, cylindricals number: 3 or fewer (0); about 5 (1); 10 or more (2).

Weight = 2.6, L = 19 (17 extra steps), CI = 10, RI = 46

A reduced number of cylindrical gland spigots is observed in such taxa as *Tengella* (Griswold et al., 1999), *Liocranoides* (Platnick, 1999), the Malagasy ctenids, *Caloctenus*, and *Gephyroctenus*. Some others have roughly 5–10 cylindrical gland spigots, for example, in some cycloctenids, zorids, *Uliodon*, *Titiotus*, *Griswoldia* (Griswold, 1991: fig. 35), *Phanotea*, and some ctenids (e.g., fig. 34e). In many others there are more than 10 spigots, for example, in *Zoropsis* and *Ctenus villasboasi* (fig. 34f).

140. Posterior median spinnerets, cylindricals

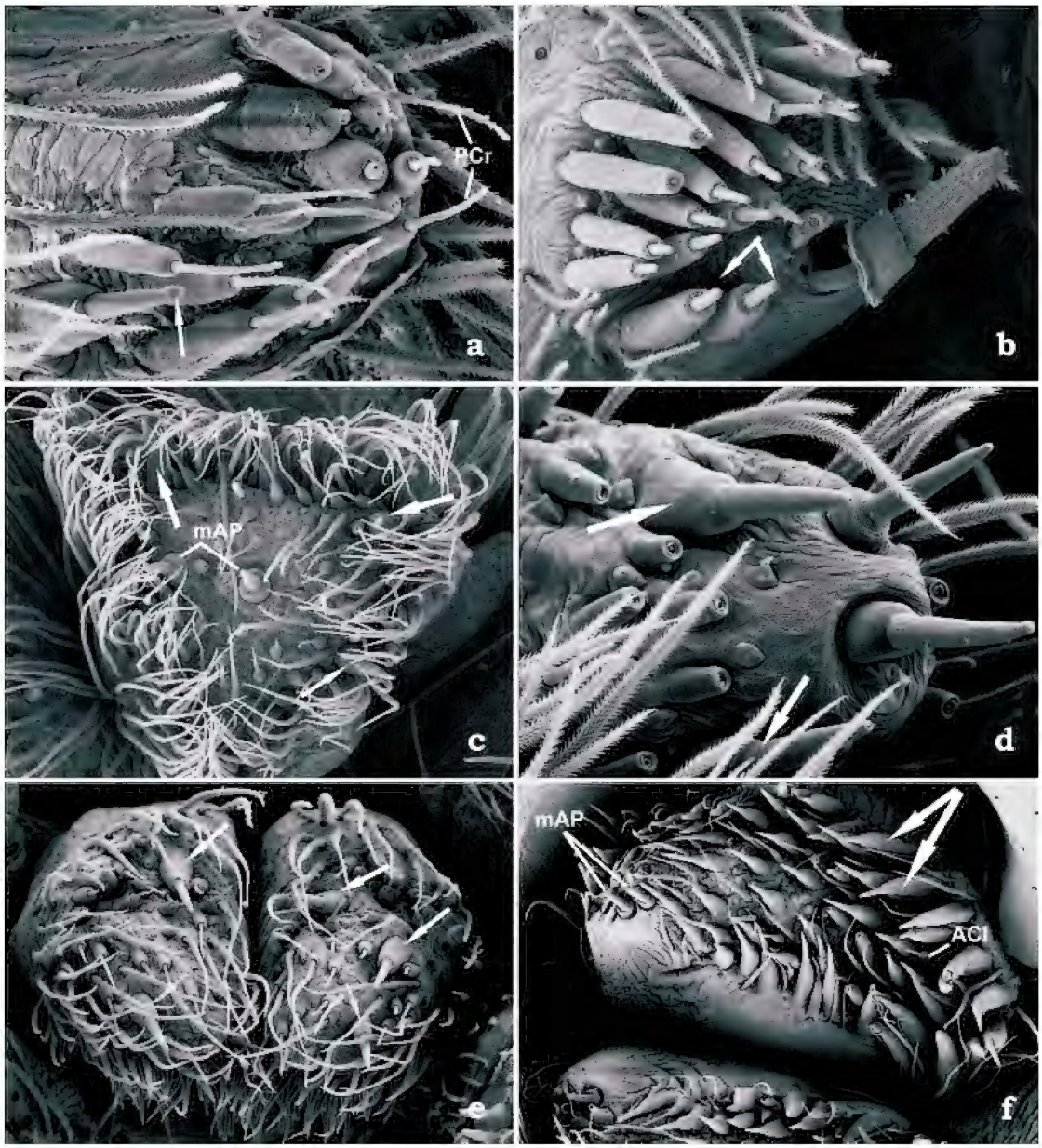

Fig. 34. Posterior median spinnerets (PMS), females. **a.** *Pimus napa* Leech. **b.** *Senoculus* cf. *gracilis* (Keys.). **c.** *Miturga lineata* Thorell, showing widely separated minor ampullate gland spigots. **d.** *Uliodon tarantulinus* (L. Koch), closeup of minor ampullate gland spigots. **e.** *Viracucha andicola* (Simon). **f.** *Ctenus villasboasi* M.-Leitão. Arrows point to cylindrical gland spigots. ACI = aciniform gland spigots, mAP = minor ampullate gland spigots, PCr = paracribellate gland spigots.

base: normal (0); greatly swollen (1); tubular (2); elongated (3).

Weight = 6.0, L = 7 (4 extra steps), CI = 42, RI = 42

Cylindrical gland spigots are recognized by being relatively larger than all other spigots (and absent in males); this is the condition in most examined taxa. However, in a few others the cylindrical bases are greatly enlarged (state 1) (e.g., *Caloctenus*, *Gephyroctenus*, and *Acantheis*); tubular (e.g., fig. 34b), as in *Senoculus* and *Peucetia*; or elongated (e.g., fig. 33f), as in some ctenines.

BEHAVIOR

141. Egg sac shape: spherical with loose silk (0); spherical with rigid walls (1); biconvex (2); plano convex (3); bell-shaped (4); irregularly flattened (5).

Weight = 6.0, L = 10, CI = 60, RI = 78

Spherical egg sacs lightly covered with silk threads loosely packed and often with dirt and debris added to them are found in *Amaurobius ferox*, some *Dolomedes* (Carico, 1973: 461), and in at least one species of *Griswoldia* (Griswold, 1991: 310). On the other hand, lycosids, as well as most pisaurids, have a spherical egg sac, although the silk threads are tightly woven (Preston-Mafham, 1998: 63). A biconvex egg sac is found in a broad range of mygalomorph and araneomorph families (Bellmann, 1997); in this study, it has been scored for trechaleids, *Neoctenus*, and most ctenids. In the former two, a leathery egg sac, dark to orange brown, is attached through a few threads to the spinnerets (Carico, 1993: 236; personal obs.), whereas in some ctenids, a papery, often whitish, biconvex egg sac is carried with the chelicerae.

A plano-convex egg sac, state 3, is observed also in a broad range of spiders, herein scored for cycloctenids (Forster and Blest, 1979: 12, fig. 39; Hickman, 1981: 50) and such ctenids as Mad 2, the New Caledonian *Anahita*, *Phoneutria*, *Ancylometes*, *Ctenus fasciatus*, and *Ctenus* cf. *sinuatipes*. State 4, a bell-shaped egg sac, appears to be unique to some liocranids, for instance, *Agroeca* (Bellmann, 1997: 172; Sauer and Wunderlich, 1997: 261; Foelix, 1996: 207, fig. 175); although it is still unknown, *Liocranum* is scored also for this condition. State 5, an irregularly flattened egg sac, is known in the clubionids and *Miturga* (Brunet, 1998: 99, 102; Sauer and Wunderlich, 1997: 259; Bellmann, 1997: 173; Roberts, 1995: 133).

142. Egg sac seam: not distinctive (0); raised (1); with skirt (2); weakly marked (3).

Weight = 10, L = 3, CI = 100, RI = 100

In many of the examined taxa, the egg sac is roughly uniform, but some others may have a seam, clearly visible when the egg sac is full of eggs, that further differentiates among lycosids, trechaleids, and pisaurids (Carico, 1993: 236). In lycosids, the egg sac has a well-defined rim (Foelix, 1996: fig. 176b), but pisaurid egg sacs lack any kind of marking; in trechaleids, the egg sac has a distinctive skirt (Carico, 1993: fig. 6) which is absent in *Neoctenus*. In many ctenids, including *Phoneutria*, a weakly marked rim often separates the two egg sac valves.

143. Egg sac: fixed (0); transported with chelicerae (1); transported on spinnerets (2) (char. 68, Griswold, 1993).

Weight = 6.0, L = 6 (4 extra steps), CI = 33, RI = 78

In most examined taxa as well as in some ctenids (F.O.P-Cambridge, 1897a: 108), the egg sac is constructed and placed on various kinds of substrates (state 0). State 1 refers to the transport of the egg sac with the chelicerae, which is recorded in *Psechrus* (Levi, 1982: 117), pisaurids (Preston-Mafham, 1998: 60; Bellmann, 1997: 141, 143; Foelix, 1996: 210), and various ctenids (Höfer et al., 1994: figs. 1d, 3b).

State 2 refers to an egg sac transported on the spinnerets. It is recorded in the trechaleids (Carico, 1993), *Neoctenus*, as well as in various lycosids (Bellmann, 1997: 145–165; Foelix, 1996: 208), even in those that rely on webs (Preston-Mafham, 1998: 26; Koh, 1989: 94; Dondale, 1986: 327); this condition, regarded as a synapomorphy for the Lycosidae (Dondale, 1986: 327), is also recorded in *Cupiennius* (personal obs.).

144. Egg sac: fixed to web (0); attached to a nonsilky substrate (1); inside silken nest (2); suspended from the vegetation by a narrow silken attachment (3).

Weight = 7.5, L = 5 (2 extra steps), CI = 60, RI = 77

State 0 refers to the condition observed in some cribellate spiders, which may attach the egg sac to their webs, as is the case in *Megadictyna* (Forster, 1970: 178), *Amaurobius* (Bellmann, 1997: 47), and *Tengella* (Eberhard et al., 1993:3).

State 1 refers to egg sacs attached to substrates different than silk. This condition is scored for some cribellates, which construct their egg sacs underneath fallen logs, loose tree bark, mosses, bromeliaceae, and such, for example, in *Zoropsis* (Bellmann, 1997: 55; Sauer and Wunderlich, 1997: 44; Levy, 1990: 142), *Acanthoctenus* (Simon, 1892: 228), and *Nothroctenus* (Calaça-Dias and Brescovit, 1999: 62). Among ecribellates, this condition is known in cycloctenids (Hickman, 1981: 50; Forster and Blest, 1979: 39), *Senoculus* (Chickering, 1941: 196; Simon, 1898: 369; personal obs.), *Zora* (Bellmann, 1997: 173; Bennett and Brumwell, 1996: 105; Simon, 1897: 134), *Griswoldia* (Griswold, 1991: 310), *Ctenus fasciatus* (Gnaspini, personal commun.), *Ctenus* cf. *sinuatipes* (Viquez, personal commun.), *Asthenoctenus* (Simó, 1994: 7), a new genus from Madagascar (Mad 2), a new species of *Anahita* (New Caledonia)—the latter two records are based on specimens collected with their egg sacs attached to leaves—and *Phoneutria* (Lucas, 1969: 37), albeit species of this genus may also transport it with the chelicerae under certain circumstances (Lucas, 1969: 38; personal obs.).

State 2 refers to the condition in *Miturga* as well as some other miturgids and clubionids. Females in these taxa construct a silken chamber underneath tree bark, inside curled leaves, and elsewhere, to place and guard the egg sac. State 3 is here scored for *Liocranum*, although it is still unknown if this genus constructs the egg sac hanging down from a narrow attachment to the vegetation, as occurs in *Agroeca*.

145. Parental care: not specialized (0); nursery web (1); spiderlings on abdomen (2); spiderlings on empty egg sac (3).

Weight = 7.5, L = 5 (2 extra steps), CI = 60, RI = 60

Parental care (i.e., guarding both the egg sac and the spiderlings after hatching) is still unknown for many of the examined taxa. However, a kind of egg sac guarding appears to be widespread in various unrelated families (Preston-Mafham, 1998a: 65; 1998b: 88; personal obs.) and is here represented by state 0; this condition is recorded for the amaurobiids, zoropsids, *Zora*, *Cycloctenus*, and such ctenids as *Ctenus fasciatus* (Gnaspini, personal commun.) and *Ctenus* cf. *sinuatipes* (Viquez, personal commun.).

State 1 refers to a condition regarded as a synapomorphy of pisaurids, despite being still unknown in most genera (Sierwald, 1990: 8; 1993: 69). The nursery web is defined as a tentlike web constructed by the female before hatching, where the egg sac is deposited to protect the offspring until they molt and are ready to disperse (Preston-Mafham, 1998: 68; Bellmann, 1997: 14; Foelix, 1996: 210). Here, this condition is scored in *Psechrus* (personal obs.) as well as in *Ancylometes* (Merrett, 1988: 200; Brescovit, personal commun.). A nursery web has been recorded also in *Peucetia* (Sierwald, 1993: 69; Preston-Mafham, 1998: 115; Whitcomb, 1962: 198).

State 2 is an unambiguous synapomorphy of lycosids (Dondale, 1986: 327); the females transport their spiderlings on the abdomen (Foelix, 1996: fig. 176e) until they disperse. State 3 refers to the condition in *Trechalea* and other trechaleids (Carico, 1993: 236); the females in this group transport the spiderlings in the empty egg sac until they disperse.

146. Foraging strategies: web snaring (0); ground ambushers (1); aquatic hunters (2).

Weight = 5.0, L = 8 (6 extra steps), CI = 25, RI = 50

State 0 was scored for all the cribellate spiders, including the three ctenid genera. With the exclusion of those genera, the great majority were scored as ground ambushers, including the lycosids, although some species may hunt on the water surface (personal obs.; Koh, 1989: 93). The aquatic life-style of *Ancylometes*, so far unknown in ctenid spiders, prompted the inclusion of character 147, treated either as an independent character or as one state in a multiple transformation series; results indicate an independent origin in such pisaurids as *Dolomedes* and *Thalassius*, as well as in *Trechalea*.

APPENDIX 2

Data Matrix of 98 Taxa and 146 Characters

"?" unknown, "-" nonapplicable

Characters:	012345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890	5555 1234
Megadictyna	000000	00000	00000	00-00	-0000	00000	00000	00000	-201-	----0	0000
Pimus napa	000100	00000	01000	00-00	-0000	00000	00000	00001	00000	00-02	0000
Amaurobius	000000	00000	01000	00-00	-0000	00100	00000	00000	-1000	00-02	2000
Cycloctenus flavus	000000	00000	01000	00-02	10000	00200	00001	00000	-0000	00-02	2100
Cy flaviceps	000100	00000	01001	00-02	10000	00200	00000	00000	-0000	00-02	2000
Cy westlandicus	000100	00000	01001	00-02	10000	00200	00000	00000	-0000	00-02	2000
Liocranum	000100	00000	01000	00-01	00000	00000	00000	00000	-0000	00-02	0300
Clubiona	000100	00000	01000	00-00	-0000	00000	00000	00000	-001-	----2	7000
Elaver	000100	00000	01000	00-00	-0000	00000	00000	00000	-00??	00-02	?000
Strotarchus	000100	00000	01000	00-?1	00000	00000	00000	00000	-0000	00-02	9000
Eutichurus	000100	00000	01000	00-?0	-0000	00000	00000	00000	-0000	00-02	0000
Teminius	000100	00000	01000	00-10	-1100	00000	00000	00000	-0001	00-02	4100
Miturga	000000	00000	01000	00-11	01100	00000	00000	00000	-0001	00-01	4100
Uliodon	000100	00000	01000	00-11	01100	00000	00000	00000	-0001	00-01	4100
Tengella	000100	00000	01000	00-11	00000	02300	00000	00000	-0000	00-02	0100
Zorocrates	000100	00000	01000	00-10	-0000	02300	00000	10000	-0000	00-02	9100
Liocranoides	000100	00000	01000	00-10	-0000	02300	00010	00000	-0000	00-12	2100
Anachemmis	000100	00000	01000	00-10	-0000	02300	00010	00000	-0000	00-12	2100
Titiotus	000110	00000	01000	00-10	-0000	02300	00000	00000	-0000	00-12	2100
Zoropsis	000100	00000	01000	00-10	-0000	02300	00000	00000	-0000	00-02	0100
Raecius	000110	00000	01000	00-10	-0000	02300	00000	10000	-0000	00-02	9100
Uduba	000110	00000	01000	00-10	-0000	02300	00000	10000	-2000	00-02	9100
Zorodictyna	000110	00000	01000	00-10	-0000	02300	00001	00000	-0000	00-02	2100
Griswoldia	000100	00000	01000	00-10	-0000	02300	00000	00001	10000	01102	0100
Phanotea	000100	00000	01000	00-10	-0000	02300	00000	00000	-0000	01102	2100
Chile	000100	00000	01000	00-10	-0000	02300	00000	00000	-0000	01102	0100
Psechrus	000000	00000	00-00	00-10	-0000	00000	00000	00000	-101-	----3	3100
Peucetia	000100	00000	00---	-0-?2	10007	00000	00000	00000	-2100	00-02	0?00
Senoculus	000100	01000	00---	-1012	10000	00000	00000	00000	-2100	00-02	0200
Se gracilis	000100	01000	00---	-0-12	10000	00000	00000	00000	-2100	00-02	?200
Lycosa	000100	00000	00---	-0-11	00000	00010	00000	00000	-2000	00-03	3100
Aglaoctenus	000100	00000	00---	-0-10	-0000	00010	00000	00000	-2000	00-03	3100
Neoctenus	000100	00100	01000	00-11	00000	000?0	00000	00000	-0000	10-03	3100
Trechalea	000100	00100	01000	00-11	00000	00010	00000	00000	-3000	10-03	3100
Thalassius	000100	00000	0?000	00-10	-0000	00011	11000	00000	-0000	00-03	3100
Dolomedes	000100	00000	01000	00-10	-0000	00011	11000	00000	-0000	00-03	3100
Ancylometes	000100	00000	01000	00-11	00000	00100	00000	00000	-1000	00-04	0100
Trujillina isolata	000101	00000	01010	00-10	-0003	00100	00000	00000	-0000	00-02	8110
Trujillina spinipes	000101	00000	01010	00-10	-0003	00?00	00000	00000	-0000	00-02	8110
Odo agilis	000100	00000	00000	01111	00000	01100	00000	10100	-0000	00-02	2110
Odo obscurus	000101	00000	01000	00-10	-0000	01100	00000	10100	-0000	00-02	0110
Odo Chile	000100	00000	00000	01110	-0000	0??00	00000	10100	-0000	00-02	0110
Argoctenus	000100	00000	01000	10-11	01000	00000	00000	00000	-000?	00-01	4100
Diallomus	000100	00000	01000	00-10	-0000	00000	00000	10000	-0000	00-02	6100
Elassoctenus	000100	00000	01000	10-11	01000	00000	00000	00010	-0001	00-01	4100
Hestimodema	000100	00000	01000	10-10	-1000	00000	00000	00010	-0001	00-01	4300
Zora spinimana	000100	00000	01000	10-11	01000	00000	00000	00000	-0001	00-01	4300

APPENDIX 2
(Continued)

Characters:	012345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890	5555 1234
Xenoctenus	000100	00000	00000	00-10	-0000	01400	00000	00000	-0000	00-02	0110
Odo lycosoides	000100	00000	01000	00-11	00000	01400	00000	10000	-0000	00-02	2110
Asthenoctenus	000100	00000	01000	00-10	-0000	00000	00001	00000	-0000	00-04	0100
Cupiennius	000100	00000	01000	00-11	00000	00000	00000	00000	-0000	00-03	2100
Anahita isaloensis	000100	00000	01000	00-10	-0002	02300	00000	00001	30000	00-00	0100
Vulsor	000100	00000	01000	00-10	-0002	02100	00000	00001	30000	00-00	4100
Viridasius	000100	10000	01000	00-10	-0010	02300	00100	00001	40000	00-02	2100
Vi fasciatus	000100	10000	01000	00-10	-0010	02300	00100	00001	40000	00-02	2100
Madagascar 2	000100	00000	01000	00-10	-0000	0?300	00000	00001	50000	00-02	0100
Madagascar 25	000100	00000	01000	00-11	00000	0?300	00000	00001	50000	00-02	0100
Nothroctenus	010100	00000	01000	00-10	-0001	02100	00000	00001	20000	00-02	5100
Viracucha	010100	00000	01000	00-10	-0001	00?00	00000	00000	-0000	00-02	2100
Acanthoctenus	010100	00000	01000	00-10	-0001	02100	00000	00000	-0000	00-02	0100
Thoriosa	000100	00000	01000	00-11	00024	02300	00000	00000	-0000	01002	0100
Australia 1	001100	00000	01000	00-10	-0020	02300	00000	00000	-0000	01002	2100
Lombok	001100	00000	01000	00-11	00020	02300	00000	00000	-1000	01002	2100
Brasil 1	000100	00000	01000	00-10	-0000	0??00	00001	00000	-0000	00-04	0100
Acantheis	000100	00000	01000	00-10	-0000	0?300	00000	00000	-0000	01002	2100
Enoploctenus	000100	00001	01000	00-10	-0000	02300	00001	00000	-0000	01002	0100
Ct miserabilis	000110	00001	01000	00-10	-0000	02300	00001	00000	-0000	01002	0100
Africactenus	0001?0	00000	01000	00-10	-0000	12?00	00000	00000	-0000	01002	?100
Petaloctenus	000100	00000	01000	00-10	-0000	1??00	00000	00000	-0000	01002	2100
Vietnam 1	000100	00000	01000	00-10	-0000	02100	00000	00000	-0000	01002	0100
Ctenus amanensis	000100	00000	01000	00-10	-0000	02100	00000	00000	-0000	00-02	?100
Ct hibernalis	000100	00000	01000	00-11	00000	0?100	00000	00000	-0000	01002	?100
Ct indicus	000100	00000	01100	00-10	-0000	0?100	00000	00000	-0000	01002	?100
Ct maculisternis	000100	00000	01000	00-10	-0000	0??00	00000	00000	-0000	01004	0100
Ct mitchelli	000100	00000	01000	00-11	00000	00?00	00000	00000	-0000	01002	0100
Ct narashinai	000100	00000	01100	00-10	-0000	02100	00000	00000	-0000	00-02	0100
Ct villasboasi	000100	00000	01000	00-10	-0000	02100	00000	00000	-0000	01104	2100
Tanzania 1	000100	00000	00-00	01210	-0000	02100	00000	00000	-0000	00-02	?100
Peru 1	000100	00000	01000	00-11	00000	0?100	00000	00000	-0000	01002	0100
Oligoctenus ornatus	000100	00000	01000	00-11	00000	0??00	00000	01000	-0000	01102	0100
Panama	000100	00000	01000	00-11	00000	0??00	00000	01000	-0000	01102	0100
Isoctenus coxalis	000100	00000	01000	00-10	-0000	02100	00000	00000	-0000	01102	2100
Phoneutria boliviensis	000100	00000	01000	00-10	-0000	02300	00000	00000	-0000	01102	0100
Celaetycheus	000100	00000	01000	00-10	-0000	0??00	00000	00000	-0000	00-02	?100
Ce cabriolatus	000100	00000	01000	00-10	-0000	0?100	00000	00000	-0000	01002	2100
Leptoctenus	000100	00000	00-00	01210	-0000	0??00	00000	00000	-0000	00-02	?101
Le byrrhus	000100	00000	01100	00-11	00000	0??00	00000	00000	-0000	01002	0100
Centroctenus	000100	00000	01000	00-10	-0000	02100	00000	00000	-0000	0?002	0100
Janusia muiri	0?????	?????	?????	?????	?????	?????	?????	?0???	?????	?????	?10?
Janusia	000110	00000	01000	00-?0	-0000	0??00	00000	00000	-0000	00-02	0101
Anahita punctulata	000100	00000	10-00	01210	-0000	0??00	00000	00000	-0000	00-00	010?
An New Caledonia	000100	00000	10-00	01210	-0000	0??00	00000	00000	-0000	00-04	0101
An blandini	000100	00000	10-00	01210	-0000	0?100	00000	00000	-3000	00-02	2101
Apolania	0001?0	00000	01000	00-00	-0000	0??00	00000	10000	-0000	00-02	????
Caloctenus	000110	00010	01000	00-10	-0030	02300	00000	10000	-0000	00-02	1100
Ca oxapampa	000110	00010	01000	00-10	-0000	02?00	00000	10000	-0000	00-02	0300
Gephyroctenus	000100	00000	01000	00-10	-1000	0?100	00000	00000	-0000	00-00	4300
Madagascar 30	000100	00000	01000	00-10	-0000	00000	00000	00000	-001-	----2	0300

APPENDIX 2
(Continued)

Characters:	555556 567890	66666 12345	66667 67890	77777 12345	77778 67890	88888 12345	88889 67890	99999 12345	99990 67890	1 11111 00000 12345	1111 0000 6789
Megadictyna	-----0	00000	01300	-0000	00000	00000	00000	01000	00000	0000-	0-00
Pimus napa	-----0	00000	02101	00010	10002	10000	00000	01014	00400	0000-	0-11
Amaurobius	-----0	00000	02101	00010	10002	10000	01000	01004	10401	0000-	0-11
Cycloctenus flavus	00-000	00000	00200	-1101	10111	16114	0110-	-0004	22120	01-0-	0-11
Cy flaviceps	-----0	00000	10200	-0411	10112	16114	0110-	-0004	21110	01-0-	0-11
Cy westlandicus	-----0	00000	10100	-1411	10112	16114	0120-	-0014	22121	01-0-	0-11
Liocranum	-----0	00000	00200	-0201	01301	10000	00300	01004	14020	01-0-	0-12
Clubiona	-----0	00000	00201	00211	11301	10000	00100	0100?	25500	01-11	1122
Elaver	-----0	00000	00101	00212	11302	10000	00100	0102?	25500	01-11	1122
Strotarchus	-----0	00000	00201	00201	11001	10000	01100	01020	15700	11-0-	0-?2
Eutichurus	-----0	00000	00301	00202	11002	10000	01100	01025	16700	11-11	1111
Teminius	00-000	00000	00201	00201	10001	10100	00100	0102?	1----	?1-11	1112
Miturga	00-000	00000	00201	10201	10001	10100	00101	01025	20501	01-11	1122
Uliodon	011000	00000	00201	10201	10001	10100	00001	01020	10501	01-11	1122
Tengella	00-100	00000	00101	10203	10002	10-00	01100	01020	21401	00111	0-22
Zorocrates	00-100	00000	00201	10212	10002	10000	01000	01020	23001	00111	1122
Liocranoides	00-000	00000	00201	10202	20011	10100	01300	01020	24021	01-11	1122
Anachemmis	00-100	00000	00201	10202	10011	10000	00000	01020	22021	01-11	1122
Titiotus	10-000	00000	00201	10202	10002	10000	01000	01020	24021	01-11	1122
Zoropsis	00-100	00000	00201	10202	10001	10000	00001	01120	24121	00111	1122
Raecius	00-000	00000	03?01	10202	10002	10000	00000	01100	02001	00111	0-22
Uduba	00-100	00000	03201	10202	100?2	10000	00000	01100	01401	00111	0-22
Zorodictyna	00-000	00000	03201	10202	20012	10000	00100	01120	00001	00111	1122
Griswoldia	012001	00000	00201	10202	10011	10000	00001	01120	23001	01-11	0-22
Phanotea	012001	10000	00201	10202	10012	10000	0?000	01120	21101	01-11	0-22
Chile	002000	10000	00201	10202	10012	10000	01101	01120	22021	01-11	1122
Psechrus	00-000	00100	00001	10203	00002	10000	00301	0101?	10400	0010-	1112
Peucetia	00-000	00002	00200	-0500	00?02	?0015	00001	11024	20400	01-0-	0-22
Senoculus	00-000	00001	04000	-0202	00502	2-013	02201	01014	27620	01-0-	0-22
Se gracilis	00-000	00001	04000	-0202	00502	2-013	02201	01024	22120	01-0-	0-22
Lycosa	00-000	00100	00201	10202	10412	10011	00101	01020	20401	01-11	0-12
Aglaoctenus	00-000	00100	00201	10202	10?01	10011	00101	01020	20401	01-10	0-12
Neoctenus	00-000	00000	00201	10203	10001	101??	00101	01020	22701	01-11	0-22
Trechalea	00-000	00100	00201	00202	00002	10000	00201	0102?	21401	01-0-	0-22
Thalassius	00-000	00100	00201	00302	10401	10?00	00201	01020	21401	01-0-	0-22
Dolomedes	00-000	00100	00201	00303	10401	10000	00201	01020	21401	01-11	0-22
Ancylometes	00-000	00000	00201	10203	20402	10112	01201	01020	21401	01-11	0-22
Trujillina isolata	00-000	00000	00201	10201	10011	10200	000??	?1022	?0211	01-??	0-?2
Trujillina spinipes	00-000	00000	00201	10201	10011	10100	00300	01022	24311	01-11	0-22
Odo agilis	00-000	00000	00201	10211	10010	10100	00100	0102?	20501	01-11	0-22
Odo obscurus	00-000	00000	00201	10211	10011	10100	00300	01022	20211	01-11	0-22
Odo Chile	00-000	00000	00201	10201	10010	10100	00300	01022	20501	01-11	0-22
Argoctenus	00-000	00000	0?200	-0201	002?0	1?11?	012??	?1022	20501	01-11	1112
Diallomus	-0-000	00000	0520?	?0201	10010	14212	?1101	11020	24020	01-0-	1022
Elassoctenus	-0-000	00000	0?201	10201	00220	1111?	0121-	-1022	24220	01-10	1112
Hestimodema	-0-000	00000	00200	-0201	002?0	11100	0011-	-1022	25220	01-??	0-12
Zora spinimana	-0-000	00000	00200	-0201	10210	11100	0011-	-1022	24020	01-10	1112
Xenoctenus	010000	00000	00201	00201	1000?	12?00	01101	01026	20501	01-11	0-22
Odo lycosoides	00-000	00000	00201	00201	10001	10000	01101	01026	20501	01-11	0-22

APPENDIX 2
(Continued)

Characters:	555556 567890	66666 12345	66667 67890	77777 12345	77778 67890	88888 12345	88889 67890	99999 12345	99990 67890	1 11111 00000 12345	1111 0000 6789
Asthenoctenus	012000	10000	00201	10202	20012	10112	01001	01020	22001	01-11	1122
Cupiennius	00-000	00100	00201	10203	10002	10112	01201	01020	21401	01-11	1122
Anahita isaloensis	00-010	00010	00201	10201	10010	10112	01201	01021	20501	01-11	1122
Vulsor	00-010	00010	00201	10201	10011	13112	01201	01021	20501	01-11	1122
Viridasius	014000	10000	00201	10201	10011	10112	01201	01021	20501	01-11	1122
Vi fasciatus	015001	10000	00201	10201	10011	10112	01201	01021	20501	01-11	1122
Madagascar 2	00-011	10000	00201	10201	10010	10?12	01201	01021	24221	01-11	1122
Madagascar 25	00-001	10000	00201	10201	10010	10112	01201	01021	24220	01-10	1122
Nothroctenus	00-000	00000	05201	10202	20002	10112	01101	11020	24120	00111	1122
Viracucha	00-000	00000	05201	10202	20002	10112	01201	11020	24020	00111	1122
Acanthoctenus	00-000	00000	05201	10202	20002	10112	01201	11020	24320	00111	1122
Thoriosa	112000	00000	00201	10203	20011	10112	01101	01020	22011	01-0-	1122
Australia 1	112000	00000	00201	10203	20012	10100	01001	01020	22011	01-10	1022
Lombok	112000	00000	00201	10203	20011	10112	01001	01020	22011	01-10	1122
Brasil 1	012000	00000	0?201	10202	20012	10112	01101	01020	22011	01-11	1122
Acantheis	112000	00000	05201	10204	20011	10112	01201	11020	24121	01-10	1122
Enoploctenus	012000	00100	05201	10203	20011	10112	01201	?1020	24021	01-11	1122
Ct miserabilis	112000	00000	05201	10203	20011	10112	01201	01020	22021	01-11	1122
Africactenus	012000	00000	05201	10203	20011	10112	01201	11020	22020	01-11	1122
Petaloctenus	112000	00000	0?201	10203	20012	10112	01201	01020	220?0	01-11	1122
Vietnam 1	112000	00000	00201	10203	20012	10112	01201	01020	22001	01-11	1122
Ctenus amanensis	112000	00000	00201	10203	20012	10112	01201	01020	22011	01-11	1122
Ct hibernalis	112000	00000	00201	10203	20011	10112	01101	01020	22011	01-11	1122
Ct indicus	112000	00000	00201	10203	20012	10112	01101	01020	22001	01-11	1122
Ct maculisternis	?12000	00000	00201	10203	20012	10112	01201	01020	22001	01-11	1122
Ct mitchelli	112000	00000	00201	10203	20012	10112	01101	01020	22001	01-11	1122
Ct narashinai	117000	00000	0?201	10203	200?2	10112	01201	01020	22001	01-11	1122
Ct villasboasi	?12000	00000	00201	10203	20012	10112	01201	01020	22001	01-11	1122
Tanzania 1	112000	00000	00201	10203	20012	10112	01201	01020	22011	01-11	1122
Peru 1	112000	00000	00201	10203	20012	10112	01201	01020	22001	01-11	1122
Oligoctenus ornatus	112000	00000	00201	10203	20012	10112	01201	01020	22001	01-11	1122
Panama	112000	00000	00201	10204	20012	10112	01201	01020	22001	01-11	1122
Isoctenus coxalis	113000	00000	00201	10203	20012	10112	01101	01020	22001	01-11	1122
Phoneutria boliviensis	112000	00000	00201	10203	20011	10112	01201	01020	22001	01-11	1122
Celaetycheus	00-000	00000	00201	10204	20011	10112	01201	01020	22021	01-10	1022
Ce cabriolatus	112000	00000	00201	10203	20011	10112	01201	?1020	22001	01-0-	1122
Leptoctenus	016000	00000	00201	10212	20011	10212	01101	?1020	22020	01-0-	1122
Le byrrhus	112000	00000	00201	10202	20011	10112	01101	01020	22011	01-11	1122
Centroctenus	112000	00000	00201	10202	20011	10112	01201	01020	22011	01-11	1122
Janusia muiri	016000	010?0	00211	10204	20612	151--	-----	-1?23	28001	01-10	1022
Janusia	016000	01000	00211	10202	20612	151--	-----	-1023	28001	01-10	??22
Anahita punctulata	016000	00000	00201	10203	20010	10212	01101	01020	22011	01-10	1122
An New Caledonia	016000	00000	00201	10203	20011	10212	01101	01020	22020	01-0-	1122
An blandini	012000	00000	00201	10202	20011	10?12	01201	01020	22011	01-11	1122
Apolania	??????	???00	0520?	?0202	200?0	10?12	011??	?102?	?432?	01-0-	1022
Caloctenus	00-000	00000	05201	10203	20010	14212	11201	11020	22620	01-10	1022
Ca oxapampa	-0-000	00000	05201	10202	20010	14212	11201	11020	24620	01-10	1022
Gephyroctenus	-0-000	00000	0520?	?0203	200?0	14212	11201	11010	27620	01-0-	1022
Madagascar 30	00-000	00000	05200	-0201	00010	1?212	01201	01013	14320	01-10	1022

APPENDIX 2
(Continued)

Characters:	111111 111111 012345	11111 11112 67890	11111 22222 12345	11111 22223 67890	11111 33333 12345	11111 33334 67890	11111 44444 12345	1 4 6
Megadictyna	000000	00000	00020	00-00	0?000	0-000	00000	0
Pimus napa	00?021	00000	00200	00-10	01000	0-000	30000	0
Amaurobius	000021	00000	00200	00-10	01000	0-000	30000	0
Cycloctenus flavus	000100	10000	0020?	0022-	01001	??0??	30010	1
Cy flaviceps	000100	10000	00??1	0022-	0?001	??0??	?0??0	1
Cy westlandicus	000100	10000	0020?	0022-	01001	?0012	?0010	1
Liocranum	1--020	00000	00??0	0012-	00?01	??0??	40030	1
Clubiona	1--020	00100	00201	1002-	00011	??1--	30020	1
Elaver	1--020	00100	00201	1002-	00011	??1--	30020	1
Strotarchus	1--020	00?00	00200	0012-	10001	??1--	30??0	1
Eutichurus	1--020	00100	0020?	0012-	10001	111--	30020	1
Teminius	1--020	00000	00200	0012-	10001	?-00-	30??0	1
Miturga	1--020	00000	00210	0012-	10001	1?0??	30020	1
Uliodon	1--020	00000	00200	0012-	00001	10010	????0	1
Tengella	011020	00000	00201	00-10	00001	0?00?	?0000	0
Zorocrates	011020	00000	00201	00-1?	0000?	12010	??0?0	0
Liocranoides	011020	00000	00201	0032-	000?1	0-000	????0	1
Anachemmis	011020	00000	00201	0022-	00001	12010	????0	1
Titiotus	1--020	00000	00201	0022-	00001	11010	????0	1
Zoropsis	1--020	00000	00201	00-10	00001	11020	?0010	0
Raecius	01?020	00000	00201	00-01	00001	0-020	??000	0
Uduba	011020	00000	00201	00-11	00001	0-020	??000	0
Zorodictyna	011020	00000	00???	00-0?	0000?	??0?0	??000	1
Griswoldia	011020	00000	00201	0022-	00001	0-010	00010	1
Phanotea	011020	00000	00201	0022-	00001	0-010	?????	1
Chile	011020	00000	00201	0022-	00001	12020	??01?	1
Psechrus	00?020	10000	00201	00-10	00001	0-02?	101-1	0
Peucetia	00?000	100?0	0?200	?022-	0?001	1?02?	60011	1
Senoculus	001000	100?0	01201	2012-	00001	12002	30012	1
Se gracilis	001000	100?0	01200	2002-	00001	??0??	3001?	1
Lycosa	011000	000?0	00101	0012-	00001	12000	112-2	1
Aglaoctenus	000000	00000	00??1	0012-	00001	110??	112-?	0
Neoctenus	0--000	00000	0020?	0022-	00001	120??	2?2-?	1
Trechalea	010000	20000	00201	0022-	00001	12000	222-3	2
Thalassius	001020	00000	0020?	0022-	00?01	120??	101-1	2
Dolomedes	001020	00000	00201	0022-	00001	12020	101-1	2
Ancylometes	011020	00000	00201	0032-	00001	12020	331-1	2
Trujillina isolata	1--010	00000	00??1	0032-	00?01	??0??	????0	1
Trujillina spinipes	1--010	00000	?0??0	00?2-	00?01	??0??	????0	1
Odo agilis	1--010	00000	00??0	0022-	00001	10010	?0010	1
Odo obscurus	1--020	00000	00??0	0012-	00?01	100??	?0??0	1
Odo Chile	1--010	00000	00??0	0032-	00?01	??0??	????0	1
Argoctenus	1--010	000?0	00100	0032-	00101	10010	????0	1
Diallomus	1--010	000?0	0020?	0132-	00101	12000	????0	1
Elassoctenus	1--010	000?0	00??0	0032-	00101	??0??	?0??0	1
Hestimodema	1--000	00000	00??0	0032-	00101	10000	????0	1
Zora spinimana	1--020	00000	00100	0032-	00101	1?021	50010	1
Xenoctenus	1--010	00000	00200	0012-	00?0?	??0??	????0	1
Odo lycosoides	1--000	00000	00??0	0012-	00001	100??	?????	1
Asthenoctenus	1--020	00000	00201	0022-	00001	110?0	??010	1

APPENDIX 2
(Continued)

Characters:	111111 111111 012345	11111 11112 67890	11111 22222 12345	11111 22223 67890	11111 33333 12345	11111 33334 67890	11111 44444 12345	1 4 6
Cupiennius	011000	00000	00201	0022-	00001	120??	132-0	1
Anahita isaloensis	1--010	00000	00??0	0012-	00001	??000	?????	1
Vulsor	1--010	00000	00200	0012-	00001	10000	?0??0	1
Viridasius	1--020	00000	00200	0012-	00001	??000	?????	1
Vi fasciatus	1--020	00000	00??0	0012-	00001	??000	?????	1
Madagascar 2	1--000	00010	?0200	0032-	00001	10000	30010	1
Madagascar 25	1--010	00010	?0200	0012-	00001	??000	3?010	1
Nothroctenus	1--020	010?0	00201	00-00	00001	12010	???10	1
Viracucha	1--010	01000	00201	00-00	00001	12010	???10	?
Acanthoctenus	1--020	01000	00201	00-11	00001	12010	???10	?
Thoriosa	1--020	00000	00201	0032-	00?01	??0?0	????0	1
Australia 1	1--020	00000	00201	0032-	00101	0-010	????0	1
Lombok	1--020	00000	00201	00?2-	00?01	??0?0	????0	1
Brasil 1	1--020	00000	00??1	0022-	00001	12010	?????	1
Acantheis	1--020	00010	10201	0022-	00001	1?011	?3??0	1
Enoploctenus	1--020	00010	10201	0022-	00001	12011	????0	1
Ct miserabilis	1--020	00010	?0201	0032-	00001	120??	?????	1
Africactenus	1--020	00010	10201	0022-	00001	12000	231-0	1
Petaloctenus	1--020	00000	00201	0032-	00001	12000	231-0	1
Vietnam 1	1--020	00000	00201	0022-	00001	12020	231-0	1
Ctenus amanensis	1--020	00000	00221	0022-	00001	120?0	??1-0	1
Ct hibernalis	1--020	00000	00201	0022-	00001	120??	?????	1
Ct indicus	1--0?0	00000	00201	0022-	00001	12010	231-0	1
Ct maculisternis	1--0?0	00000	00201	0022-	00001	120??	231-0	1
Ct mitchelli	1--020	00000	00201	0022-	00001	11013	?????	1
Ct narashinai	1--0?0	00000	00???	0022-	00001	??0?0	?????	1
Ct villasboasi	1--020	00000	00201	0032-	00001	12023	231-0	1
Tanzania 1	1--020	00000	00201	0022-	00001	12010	231-0	1
Peru 1	1--020	00000	00201	0022-	00001	12013	231-0	1
Oligoctenus ornatus	1--020	00000	00201	0022-	00001	120??	23010	1
Panama	1--020	00000	0020?	0022-	00001	1-020	23??0	1
Isoctenus coxalis	1--020	00000	00201	00?2-	00001	120??	2?1-0	1
Phoneutria boliviensis	1--020	00000	00201	00?2-	00001	??0?0	331-0	1
Celaetycheus	1--020	00000	00???	0032-	00?01	??0??	????0	1
Ce cabriolatus	1--0?0	00000	00??1	00?2-	00?01	??0??	????0	1
Leptoctenus	1--0?0	00000	00???	0032-	00?01	??0??	?????	1
Le byrrhus	1--020	00000	00201	00?2-	00?01	??0??	?????	1
Centroctenus	1--020	00000	0020?	0022-	00001	0?000	231-0	1
Janusia muiri	0110?0	00000	00???	0032-	00??1	??0??	?????	1
Janusia	011020	00000	00???	0012-	00001	??0?0	?????	1
Anahita punctulata	1--020	00000	00221	0032-	00001	120?0	????0	1
An New Caledonia	1--0?0	00000	?022?	0032-	00001	12010	33010	1
An blandini	1--020	00000	00201	0022-	00001	0?010	????0	1
Apolania	1--020	000?0	00?0?	0??2-	00101	??00?	????0	1
Caloctenus	1--010	00011	00201	0112-	00001	0-001	????0	1
Ca oxapampa	001010	00011	0020?	0122-	00001	??0??	????0	1
Gephyroctenus	1--010	00011	10201	0122-	00101	?-001	????0	1
Madagascar 30	1--010	00011	10???	0112-	00001	11000	?????	1